A CONTRIBUTION TO THE NATURAL CLASSIFICATION OF LOWER AND MIDDLE CAMBRIAN ARTHROPODS: FOOD-GATHERING AND FEEDING MECHANISMS.

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ABSTRACT

The classification of arthropods and arthropodlike invertebrates of Lower and Middle Cambrian strata is currently in a state of flux. Reanalysis of these early arthropods, however, indicates that a more widely acceptable basis for their natural classification might emphasize mechanisms of food gathering and feeding. Moreover, such mechanisms are usually readily determinable in both fossil and living specimens.

This study employs a relatively broad definition of the term "arthropod", and utilizes most higher classificatory names of the arthropod literature, but with reorganized emphasis. The views of Gould (1989) and Briggs et al. (1993) concerning high-level taxonomic diversity (disparity) of Lower and Middle Cambrian arthropods (sensu Walcott, 1912) are generally supported. However, these taxa have all been classified previously within accepted arthropod subcategories and none is considered new at the level of phylum or subphylum. Although the present analysis suggests plausible evolutionary pathways for food-gathering and feeding mechanisms in uniantennate (i.e., chelicerate) lineages, and possibly in biantennate (i.e., crustacean, myriapod and hexapod) arthropods, incorporation of these ideas within a suggested formal classification awaits broader acceptance among current workers.

INTRODUCTION

Arthropods are a major component of a fauna that, during the Cambrian Period, attained what has been described by Gould (1989) as a "maximum disparity of animal life". This concept, of broad morphological diversity at high taxonomic level (here defined as subclass or higher, or undetermined), has been questioned in detail by several (e.g., Ridley (1990, 1993; Briggs et al. (1992), but ably defended by Gould (1993) and Foot & Gould (1992). Thus, disparity of arthropods and arthropod-like forms does not appear to have been greater in Cambrian than in Recent times, whatever classifications are consulted or methodologies used (Wills et al., 1994). However, in proportion to the small number (<100) of Cambrian arthropod species recorded to date, from a half dozen or so major fossil sites world-wide, the percentage of high-level taxa that they represent is very much higher than that of comparable samples of Recent faunas. If considerations are restricted to aquatic faunas only, the percentage difference is even higher. Whatever the magnitude of these differences, however, the Cambrian Period can fairly be viewed as the period of arthropod evolutionary "explosion".

Cambrian arthropods are mostly unlike living representatives of the phylum, and therefore difficult to classify on existing natural bases. One of the richest arthropod assemblages, of about 35 species, has been described from Middle Cambrian Burgess Shale deposits in Yoho National Park, British Columbia (Conway Morris & Whittington, 1985). General and popularized treatments of that fauna, by Gould (1989) and Briggs et al. (1993), have summarized the original work of Charles Walcott (1912), and the subsequent careful descriptive treatments by Whittington (1971, 1975), Bruton (1981), Briggs (1979, 1981); Briggs & Whittington (1983, 1987), Collins (1987a,b), Collins & Rudkin (1981), Conway Morris (1986) and others. Their work has made possible the present re-analysis of the early arthropod fauna for which the author feels most grateful.

Previous work has revealed a plethora of Cambrian taxonomic oddities several of which, according to Gould (1989), may require new higher classification, even at the level of phylum. Gould accepted, justifiably, the morphological interpretations of the aforementioned principal workers in this unfolding paleontological drama. Recent field work, especially in the Chengjiang region of southern China (Hou et al, 1991), and in Greenland (Conway Morris et al, 1987), has yielded many more important new taxa (e.g., by Hou, 1987 a, b; Hou & Bergstrom, 1991; Chen, et al. 1994). During his relatively brief two-year book-compilation period, Gould (1989) touched on the initial papers by Hou; however, he did not reference other pertinent works of group specialists (e.g. of Bergström, 1986; Schram, 1986; Dahl, 1984, 1987) that embody alternative and possibly more plausible classifications and evolutionary starting points, as suggested by the writer (Bousfield, 1987), for some of the major Burgess arthropod groups. Some reviewers (e.g., Fortey, 1989) have pointed to papers on cladistic classificatory methodology (e.g., Briggs & Fortey, 1989) that do provide credible, but not entirely correct, classifications of some of the enigmatic groups contributing to Gould's high disparity levels.

Delle Cave & Simonetta (1991) analyzed previous studies in a well illustrated and comprehensive account of early Paleozoic arthropods. They emphasized the importance of functionality, specially the the role of feeding appendages in the evolution of arthropod morphotypes. For the most part, their taxonomic groupings and evolutionary charts bring perceptive and cohesive insight to some mini-groups (e.g., trilobitomorphs, the *Sanctacaris* problem, and the Scanian larval stages), and stress the need for authors to name new taxa, whatever the later higher categories might be. However, they did not differentiate between food gathering and feeding (masticatory) roles and, as summarized in their

Table IV, apparently missed the significance of relationships within the Dicephalosomata and the overall relationships between anomalocarids and primitive trilobitomorph assemblages (which they did recognize) such as the Yohoiida and Leanchoiliida. Briggs et al (1993) continued with a conservative classification of early arthropods (p. 6) in which several previous higher taxa were not recognized and the anomalocarids omitted entirely. Whatever the merits or weaknesses of these various treatments, collectively they underscore the state of flux that presently characterizes early arthropod classification.

The purpose of this paper is to provide a classification that reflects more closely the actual degree of biological disparity and the major evolutionary themes within the Cambrian arthropod fauna. It also attempts to reveal, in more detail than previously, the relationship between form and food-gathering and feeding functions in selected Lower and Middle Cambrian arthropods and their descendent groups.

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In the preparation of composite illustrations here I have been privileged to adapt, with warmest appreciation, the original text illustrations of D. E. G. Briggs, H. B. Whittington, D. E. Collins, F. R. Schram, X. Hou, L. Delle Cave, A. Simonetta, and several other primary sources.

In parallel to the present study, Professor Edward Laidlaw Smith, San Francisco, CA, has combined and collated previous arthropod categories in a detailed phyletic classification of arthropods (Atlas of Insect Anatomy, unpublished). Since this study has resulted in some similar classificatory conclusions, Dr Smith has generously permitted detailed reference to and use of updated non-insect arrangements in this text, for which I am most grateful.

SYSTEMATIC PREAMBLE

The term "arthropod" is here defined as an invertebrate having an externally segmented body that bears one or more pairs of jointed appendages. The body consists of head and trunk regions, of which the latter may be tagmatized or subdivided into thorax and abdomen, mesosome and metasome, pygidium and/or telson, according to the taxonomic group. In primitive aquatic arthropods, the head always bears an acronal segment (first, or protocerebral somite) that is always pre-oral in position, having sensory organelles but no jointed limbs. The first true head segment (second or deutocerebral somite) is limb bearing, and usually pre-oral in active life stages. The head may also encompass up to five (rarely six) additional limb-bearing segments, the first of which (third or tritocerebral somite) may appear pre-oral in position. The post-oral appendages of head and trunk are primitively or embryologically biramous, the segments of which are externally chitinized, sclerotized or mineralized. The inner ramus is usually locomotory, food gathering or masticatory, and the outer ramus usually respiratory in function. Growth proceeds by moulting of the ectoderm (ecdysis). Following Bergström (1986, 1987) and Chen et al. (1994), true arthropods here embrace the primitive Cambrian dicephalosomatid genera *Anomalocaris, Opabinia, Cassubia* and close relatives. However, contrary to the views of Snodgrass (1956) and Manton (1977), true arthropods do not include the Tardigrada nor the Onycophora in which the body is not externally segmented and the post-oral limbs, although dactylate (clawed), are not jointed nor biramous.

The Middle Cambrian macro-arthropod fauna is characterized by a high percentage of primitive body forms that, superficially, appear to be intermediate between true worms (phylum Annelida) and higher groups of aquatic arthropods such as the Chelicerata and Crustacea. Paradoxically perhaps, some of these early forms (e.g., *Opabinia*) show a remarkably high degree of specialization of body form and function that tends to mask their true phyletic affinities. In adult stages of some primitive modern arthropods (e.g., Remipedia) and larval stages of cirripedes, phosphatocopine ostracods and skaracarids, the acronal segment bears conspicuous frontal organs or frontal filaments of presumed sensory function, and/or a median naupliar eye (Schram, 1986). The acronal somite is especially well developed in skaracarid crustacean larvae (e.g., *Martinssonia* Müller & Walossek, 1986). However, in arachnids, myriapods and hexopods, the acron is considered embryonic and fused with the second head somite in active life stages (Savory, 1964).

The first true head segment (second somite) of arthropods bears one pair of limbs, of 1-14 basic segments, that is embryonically uniramous and pre-oral. These limbs may be stout, the segments spinose or toothed, or apically pincer-like and raptorial in function, as in chelicerates and their presumed precursors. However, more often they are filamentous and sensory in function, as in the "antennae" of trilobites, and the antennules of crustaceans and their presumed ancestors, and marrellomorphs. In some Cambrian arthropods (e.g., *Leanchoilia*), the appendage appears distally multi-flagellate. In higher crustaceans (Malacostraca), the antennules are often secondarily biramous (e.g., in Eumalacostraca), and occasionally triramous (in Stomatopoda). In myriapods and insects, the antennae are uniramous, filamentous and sensory. In no instance, however, are these appendages gnathobasic.

The third head somite (rarely lacking except in a few Cambrian species such as *Opabinia* and *Sidneyia*) bears a pair of limbs homologous with the antennae of crustaceans and early biantennate arthropods. These limbs, homologous also with the pedipalps of chelicerates and pycnogonids, may be uniramous or, as in the intercalary (supralingual) segment of myriapods and hexapods, vestigial or essentially lacking. In primitive arachnids and early precursors, and in larval stages of crustaceans, limbs of the third head somite are masticatory as well as locomotory and/or respiratory in function. Thus, as will be demonstrated in Cambrian aquatic arthropods (below), the evolutionary trend in functioning of the first two pairs of appendages in arthropods progresses from food gathering and mastication, to food sensing and tactilility.

The head segment and limb homologies employed in this study, and suggested classification (pp. 23-27), conform with classical concepts of arthropod head structure, innervation and embryology (e.g., of Borradaile & Potts, 1941; Savory, 1964; Bergström, 1979). Kukalova-Peck (1987) and Smith (1990) have fused the acronal segment of hexapods with the labrum to form the clypeolabral, or first (protocerebral) somite which, in Upper Carboniferous monurans, appears basolaterally segmented. The second head somite remains the antennal (deutocerebral) somite, homologous with the antennular somite of crustaceans. However, Smith (loc. cit.) has suggested that the chelicerae of arachnids originate on the third (tritocerebral, supralingual) somite, and the pedipalps on the fourth or mandibular segment, resulting in eight prosomal somites, one more than the normal maximum recognized by all other authors.

In Cambrian arthropods, the anterior portion of the gut is typically deflexed and the mouth usually opens ventrally on the head. In a few groups, however, (e.g., *Jianfengia, Sanctacaris*) the mouth appears to open apically or frontally (Hou, 1987a, Briggs & Collins, 1988). Body segmentation may not always be externally visible, especially in larval forms, or in highly modified adults (e.g., some internal parasites). Paired limbs of the trunk are primarily biramous, but may be secondarily uniramous. The branches may be variously modified, unsegmented, or lacking (e.g., in early growth stages and in adults of various taxonomic groups). Thus, in a biramous limb, the outer branch may be lightly chitinized and flaplike (unsegmented) in swimming forms or, when the outer is respiratory in function, the inner branch may be fully segmented, leglike, and heavily calcified or mineralized, especially in heavy bodied benthic forms. As noted above, some post-oral paired appendages may be gnathobasic wherein the coxa and/or adjacent segments are medially toothed, or the entire limb reduced and modified as a specialized mouthpart (e.g., mandible or maxilla). Such feeding appendages are tagmatized as part of the cephalon.

Morphological differences between major groups of arthropods are fully as great as between accepted subphyla and classes within other major phyla (e.g., as between chitons and cephalopods within phylum Mollusca). In Lower Cambrian to Lower Ordovician times (530-500 m.y.b.p.), major groups of arthropods having modern representatives (e.g., Chelicerata, Crustacea) were then in what might be termed a primordial or early state of evolution or, in the case of Myriapoda and Hexapoda, unrecognized as such. Thus, true crustaceans were represented in the Cambrian fossil record only by the Maxillopoda (Ostracoda, Cirripedia, and skaracarid larval forms) (see Schram, 1986 in part; Dahl 1984, 1987). Members of the Aglaspida (Upper Cambrian) were considered by Bergström (1979) to be early chelicerates but Briggs et al. (1978) demonstrated the filamentous nature of the "chelicerae" and removed the Aglaspidida from the merostomes. The earliest chelicerates are *Chasmataspis*, or perhaps *Triopus*, from the Lower Ordovician (Fig. 8). Other major arthropod groups (e.g. Myriapoda, Hexapoda) were recognizable in late Silurian and early Devonian times, when freshwater and terrestrial fossils deposits were first identiifed.

PREVIOUS CLASSIFICATIONS

Several different classifications of Cambrian macroarthropods have been proposed, four of which are presented in Table I. The 17 sample species listed here were classified initially by Walcott (1912) who "shoehorned" them (*fide* Gould, 1989) into a relatively few existing crustacean and arachnid subcategories (Column 1). Over the next 75 years the species were classified variously by Störmer (1959), Sharov (1966) and Bergström (1979), and incorporated by Edward Laidlaw Smith in a forthcoming "Atlas of the Insecta", communicated to the writer, with kind permission, for comparative purposes here (Column 4). Despite previous designations, Gould (1989) regarded these forms as highly distinctive, belonging to two new phyla; 12 unique arthropods; one chelicerate arthropod; one trilobite; and one malacostracan (Column 2). Briggs et al.(1993) had retreated into a somewhat similar conservative listing of Cambrian arthropods, a list that did not include *Anomalocaris, Opabinia*, and other dicephalosomatid forms (Column 3). The E. L. Smith listing (Column 4) would place 15 of Gould's new or unique taxa within long-established classes of crustaceans, trilobitoids, protochelicerates, and chelicerates, five of them more or less within Walcott's original categories. However, as we may note in the following text, Smith's placement of *Marrella* and*Branchiocaris* within the protochelicerates, and *Odaraia* and*Canadaspis* within the Crustacea, is interpreted otherwise here.

Mechanisms of food-gathering and feeding.

In assessing the overall legitimacy of these classifications, we might conclude that, under the circumstances of the relatively limited systematic knowledge of his day, Charles Walcott was remarkably perceptive in much of his classification. Although the reticence of Gould and Briggs to refine

TABLE I. THE CLASSIFICATORY STATUS OF SOME BURGESS SHALE FOSSIL GENERA

Genus Name	**Higher category by Author**			
	Walcott (1912)	**Gould (1989)**	**Briggs et al (1993)**	**E.L.Smith ("Atlas" prep)***
Marrella (Walc.)	near Trilobita	unique arthropod	Arthropod (primitive)	Protochelicerata Stormer, 1944 CL. Marrellidea Walcott 1912
Yohoia (Walc.)	branchiopod crustacean	unique arthropod	Arthropod (other)	Protochelicerata Størmer, 1944 CL. Yohoiidea Henriksen 1928
Opabinia (Walc.)	branchiopod crustacean	new phylum	Unassigned Invertebrate	Protochelicerata Størmer, 1944 CL. Probosciferidea Sharov 1966
Burgessia (Walc.)	branchiopod crustacean	unique arthropod	Arthropod (other)	Trilobitoidea Størmer, 1955 O. Nectaspida Raymond, 1920
Branchiocaris (Walc.)	malacostracan crustacean	unique arthropod	Arthropod (primitive)	Protochelicerata Størmer 1944 CL. Branchicaridea
Canadaspis (Walc.)	phyllocaridan crustacean	malac- ostracan	Crustacea	Crustacea Pennant 1777 CL. Branchiopoda Latr. 1817
Naraoia (Walc.)	branchiopod crustacean	soft-bodied trilobite	Trilobita	Trilobitoidea Størmer, 1955 O. Nectaspida Raymond 1920
Odaraia (Walc.)	malacostracan	unique arthropod	Crustacea	Crustacea Pennant 1777 CL Pranchiopoda Latreille, 1817
Sidneyia (Walc.)	merostome	unique arthropod	Arthropod (other)	Protochelicerata Størmer 1944 CL. Sidneyiidea Walcott,1912
Molaria (Walc.)	merostome	unique arthropod	Arthropod (other)	Trilobitoidea Størmer, 1955 *incertae sedis*
Habelia (Walc.)	merostome	unique arthropod	Arthropod (other)	Trilobitoidea Størmer, 1955 *incertae sedis*
Actaeus (Walc.)	unknown	unique arthropod	Arthropod (other)	Protochelicerata Størmer, 1944 CL. Leancholiidea Raymond!
Alalcomanaeus (W.)	unknown	unique arthropod	Arthropod (other)	Protochelicerata Størmer, 1944 CL. Leanchoiliidea Raymond!
Emeraldella (Walc.)	merostome	unique arthropod	Arthropod (other)	Protochelicerata Størmer, 1944 CL. Emeraldellidea Raymond!
Leanchoilia (Walc.)	branchiopod crustacean	unique arthropod	Arthropod (other)	Protochelicerata Størmer, 1944 CL. Leanchoiliidea Raymond!
Sanctacaris (Briggs & Collins)	N/A	chelicerate	Chelicerata arthropod	Chelicerata Heymons 1901 Arachnida Lamarck, 1801
Anomalocaris (Walc.) + ***Laggania*** + ***Peytoia*** + appendage F	branchiopod	new phylum	Unassigned Invertebrate	Protochelicerata Størmer, 1944 CL. Anomalocaridea Raymond!

* Selected names with permission of E. L. Smith (references not detailed here); ! - Raymond, 1935.

the classification with new terminology is to some extent justified, Smith's listing of previous formal categories indicates that their reticence does not provide a helpful solution to the problem. The need seems greatest for more careful and more rigorous definition of existing categories, based on principles of functional morphology where possible, and a resort to new categories when existing or redefined categories prove inadequate. As Gould (per Schram, 1990) reminds us, errors and oversights of the past are part of the process of getting the probably correct answer, and so provide a prime stimulus for the present undertaking.

Gould (1989) noted that previous workers on Cambrian arthropods seemed reasonably confident of their classification of the most primitive forms, e.g., the Onycophora, and the presumably most advanced major taxon, the Trilobita. However, they seemed less certain of other arthropods variously attributed to the Crustacea (ie. Canadaspidida, Branchiocarida) or having only general similarities with the Trilobita. The greatest difficulties were encountered with forms having both annelid-like and arthropod-like features (e.g. *Anomalocaris*, *Opabinia*). Charles Walcott (1912) utilized subcategories of extant arthropod groups (e.g., Branchiopoda, Ostracoda + Merostomata). Størmer (1944, 1959) proposed new "catch-all" categories (e.g., Trilobitoidea) for many enigmatic forms. These classifications utilized standard character states such as body tagmatization, number of paired head (or head shield) appendages, types of appendages (biramous, gnathobasic, gill-like) and larval biology, to the limit of existing knowledge, but did not emphasize functionality or possible behavioural significance.

Bergström (1979, et seq.) employed the term "Schizoramia" to encompass all Trilobitomorpha (Trilobita, Merostomatoidea, and Chelicerata). These are characterized by primitively biramous trunk limbs of which the endopod is gnathobasic, and the exopod bears lamellar spines. The enigmatic genus *Emeraldella,* having gnathobasic post-oral legs, was included here, as well as the Marrellomorpha, but the latter group primarily lacks gnathobasic limbs. The Pycnogonida (Pantopoda) was not related to any particular arthropod group. Commendably, Bergström relegated *Opabinia* and *Anomalocaris* to the status of a "pre-arthropod" stock, but later (1986, 1987) decided they were indeed arthropods, a view now firmly supported by the recent work of Chen et al (1994). However, Bergström employed the term Uniramia to encompass both the soft-bodied, externally annulated onychophorans, and the hard-bodied, externally segmented myriapods and hexapods having whole-limb jaws. This concept is now proving flawed and untenable as a category of natural classification (see Kukalova-Peck, 1992). Onychophorans, early forms of which did exist in Cambrian seas, resemble the Tardigrada in having shaft-like, primitively uniramous limbs and pharyngeal teeth or spines, whereas myriapods and insects have segmented, primitively biramous limbs, and mouthparts modified from biramous limbs. Furthermore, Bergström's doubts that biramous and mandibulate crustaceans arose from the same gnathobasic limb stock as hexapods are not supported here nor by some other workers (e.g., Kukalova-Peck, 1987). Imperfect fossilization has so far prevented determination of the precise nature of locomotory limbs of dicephalosomatids However, such is not here considered a major impediment to phyletic implications of the better preserved, clearly "arthropodized" feeding appendages of the head region, nor overall relationships with confirmed early biramous arthropod groups.

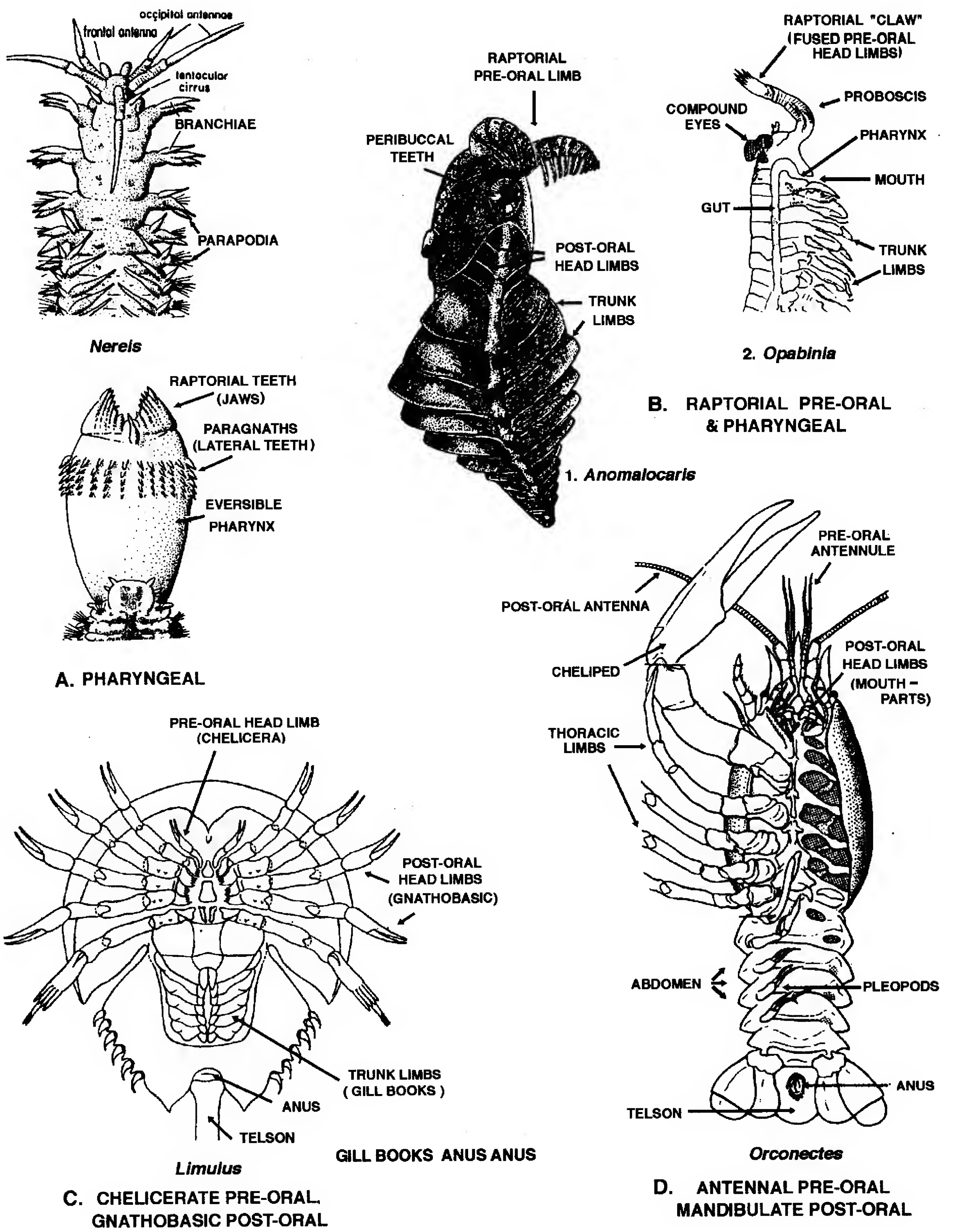
In assessing the impact of feeding processes on the evolution of body form in arthropods, a definition of terms is prerequisite. The entire feeding process encompasses food-gathering and food-consumption mechanisms. The food-gathering mechanism is the process by which food items are entrapped and brought to the mouth region. The food-consumption (feeding) mechanism is the process of mastication, the external means by which food items are rendered suitable for entry into the digestive tract proper.

Basic types of feeding processes of arthropods and their presumed antecedents are illustrated in Fig. 1. In errant polychaete worms (e.g., *Nereis, Neathes*), a taxonomic group "classically" presumed ancestral to the arthropods, the head consists of a prostomium and usually a peristomial segment bearing food-sensing tentacles. No paired limbs, segmented or otherwise, are involved in food gathering or in food mastication; these processes are entirely pharyngeal (Fig. 1A). The mechanism consists of an eversible pharyngeal proboscis, the everted distal end of which is armed with strong teeth or "jaws" by means of which the food material (prey organism) is captured and killed. As the proboscis retracts, it re-inverts, taking in the prey and partly macerating it by means of other teeth lining the pharynx wall. The food is then passed rearward to the digestive gut proper. No true arthropods conform with this category.

In very primitive uniantennate arthropods, (e.g., *Anomalocaris,* Fig. 1B.1), food is gathered by the large, spinose and multi-segmented, pre-oral paired appendages. These capture and transfer prey organisms posteriorly to the mouth region that opens immediately behind the first true head segment. The actual feeding mechanism, however, remains entirely pharyngeal; no paired mouthparts or leg gnathobases are present, although in the related *Opabinia regalis* (Fig. 1B.2), some prey items may be partly macerated by the pre-oral clawed appendage. In the anomalocarids, food is initially macerated by means of peribuccal teeth, and/or stout teeth or spines lining the anterior walls of the pharynx, as in some polychaetes. This feeding process is analogous, or perhaps even homologus, to mechanisms elsewhere among living arthropods in the pycnogonids, and among other invertebrates in the cephalopod molluscs (Borradaile & Potts, 1941). In cephalopods, the "head-foot" appendages (tentacles) grip, but do not masticate, the prey by means of specialized suckers, rather than spines; modified anterior pharyngeal teeth, the horny beaks, and smaller radular teeth masticate the prey items just inside the mouth entrance.

In more advanced uniantennates (e.g. in chelicerates, Fig. 1C), food gathering is also the prime function of post-oral head (prosomal) appendages, and/or the cheliform pair of pre-oral appendages. In primitive aquatic chelicerates (e.g., merostomes), the food is first macerated externally by means of a grinding action of the gnathobasic coxae of the paired head and/or trunk appendages. In more advanced terrestrial arachnids that secondarily lack leg gnathobases, the killing bite and maceration of the prey is performed by the distally clawed first post-oral appendages, the pedipalps and/or the pre-oral chelicerae (Savory, 1964).

Within advanced biantennate (mandibulate) arthropods (e.g., malacostracan crustaceans, Fig. 1D), the pre-oral and first post-oral appendages are flagellar and food-sensing. Food is gathered mainly by the anterior trunk (thoracic) limbs. Swimming, and often respiratory functions may be relegated to the posterior trunk (abdominal) limbs. Food is macerated by specialized post-oral limbs of the head region, the mandibulate mouthparts. Other branches or lobes of post-oral head appendages may serve in locomotion, and/or respiration, especially in adults of more primitive groups (e.g., cephalocaridans) and in larval stages of advanced forms. Food mastication may also become the primary function of one to three pairs of anterior trunk limbs, serving as maxillipeds (e.g., in Decapoda), or as gnathopods (e.g., in Amphipoda). In their larval stages (e.g., nauplii, metanauplii) the biramous first post-oral appendage (antenna 2) usually retains a function in food gathering and mastication, as well as locomotion (Schram, 1986).



A. PHARYNGEAL

B. RAPTORIAL PRE-ORAL & PHARYNGEAL

C. CHELICERATE PRE-ORAL, GNATHOBASIC POST-ORAL

D. ANTENNAL PRE-ORAL MANDIBULATE POST-ORAL

FIG. 1. BASIC TYPES OF FOOD-GATHERING AND FEEDING MECHANISMS IN AQUATIC ARTHROPODS. A. Polychaete (ancestral). B. Primitive uniantennate arthropod. C. Advanced uniantennate arthropod D. Advanced biantennate arthropod

TABLE II. SELECTED GENERA OF CAMBRIAN UNIANTENNATE ARTHROPODS CATEGORIZED BY FOOD-GATHERING AND FEEDING MECHANISMS

SEGMENTED LIMBS LACKING I.	SEGMENTED PRE- AND POST-ORAL LIMBS			
	II. PRE-ORAL LIMBS RAPTORIAL	III PRE-ORAL LIMBS TRANSITIONAL	IV. PRE-ORAL LIMBS FILAMENTOUS	V. PRE-ORAL LIMBS CHELICERATE
PHARYNGEAL MASTICATION	PHARYNGEAL MASTICATION	TRANSITIONAL PHARYNGEAL MASTICATION	GNATHOBASIC MASTICATION	GNATHOBASIC MASTICATION
POLYCHAETA TARDIGRADA ONYCHOPHORA *Hallucigenia* *Aysheaia*	ENDOPODS LOBATE OR SMOOTH *Anomalocaris* *Laggania* *Opabinia* † *Tullimonstrum* *Cassubia* *Jianfengia* *Yohoia*	ENDOPODS SPINOSE *Leanchoilia* *Acanthomeridion* *Actaeus* *Alalcomanaeus*	*Sidneyia* *Burgessia* *Molaria* *Habelia* *Tegopelte* *Naraoia* TRILOBITA *Sanctacaris* *Emeraldella* *Aglaspis*	*Chasmataspis* † MEROSTOMATA † EURYPTERIDA † SCORPIONIDA † PYCNOGONIDA ?

† Ordovician and later ? Head limbs not gnathobasic

Selected uniantennate arthropods of the early Paleozoic are grouped according to categories of food gathering and feeding outlined in Table II. As noted previously, unassisted pharyngeal feeding typifies polychaetes and pararthropods such as the tardigrades and onychophorans (Column I). The dicephalosomatid arthropods (Column II) utilize only raptorial pre-oral appendages in food gathering and/or preliminary food mastication. They feed in an essentially similar pharyngeal manner, except that the mouth opening is deflexed ventrally in anomalocarids and proboscoideans, and opens anteriorly (or nearly so) in Yohoiida (Hou, 1987a). In primitive trilobitomorphs, the Leanchoiliidacea (Column III), the post-oral head and trunk limbs appear capable of capturing and holding food items but feeding is still essentially pharyngeal. In the advanced species *Alalcomenaeus*, post-oral limbs are essentially gnathobasic (Delle Cave & Simonetta, 1991). In advanced trilobitoideans, includin *Sidneyia*, the Burgessiida, trilobites, Emeraldellida and Sanctacarida (Column IV), the pre-oral appendages become essentially singly filamentous in form and presumably chemosensory and thigmotactic in function. The post-oral head and trunk limbs become fully gnathobasic (although remaining biramous) and presumably assisted in both food capture and food mastication. The chelicerates are a final stage in the uniantennate feeding series (Column V). The raptorial pre-oral limbs are reduced to two to four segmented chelicerae, and the post-oral head limbs are fully gnathobasic and essentially uniramous. Both types of head appendages may assist in food gathering and food maceration, especially in the terrestrial arachnid subgroups. The anterior post-oral trunk limbs are essentially uniramous; the endopod is lost, but the exopod remains functional in respiration.

This tabular arrangement of taxa according to feeding style parallels an increasing evolutionary sophistication of head and trunk segmentation, and form and function of their appendages as detailed in pages 11-14. It also matches the fossil track record of the uniantennate groups (Table V, p. 28). Thus, the most primitive feeding styles, as in the dicephalosomatids, persisted little beyond the Cambrian Period and not beyond the Palaeozoic Era. By contrast, the most advanced uniantennate feeding types expanded into the chelicerate taxa of Ordovician and later periods, including the remarkably diverse terrestrial arachnids of Tertiary and Recent times.

Evolution of Post-oral Limb Morphology

The changing structure of the post-oral head and trunk appendages of uniantennate arthropods is depicted in greater detail in Figure 2. Within the Dicephalosomatida, the Anomalocarida and Probosciferida were equipped with pairs of closely approximated paddlelike plates on each side, not clearly joined at the base, and perhaps not technically, even if functionally, forming a biramous limb. The upper plate (in *Opabinia*, Fig. 2B, C) was fringed with lateral lamellae, presumably respiratory in function. The head of *Opabinia* (2B, C; 7C.1)lacked post-oral plates, but the three pairs of post-oral head plates in *Anomalocaris* (Fig. 2A) are considered homologus with the trunk plates. In *Cassubia* (Fig. 3), considered here (and by Smith, "Atlas" unpubl.) as a benthic anomalocarid with relatively short stout pre-oral limbs, the head may be two segmented. Trace elements alongside the trunk may be ambulatory endopods of the posterior head and/or anterior trunk segments. In Yohoiida, including the multi-segmented *Jianfengia* from the Lower Cambrian of China (Fig. 7G), the head bore 3 pairs of post-oral appendages of which the endopod was 7-segmented, cylindrical, and presumably ambulatory. The limbs were not demonstrably gnathobasic, but the ectoderm was sclerotized or mineralized, with a gill-like exopod, much as in a trunk limb of the biantennate genus *Marrella* (Fig. 2D). An exopod was present and foliaceous in head limbs of the elongate *Jianfengia*

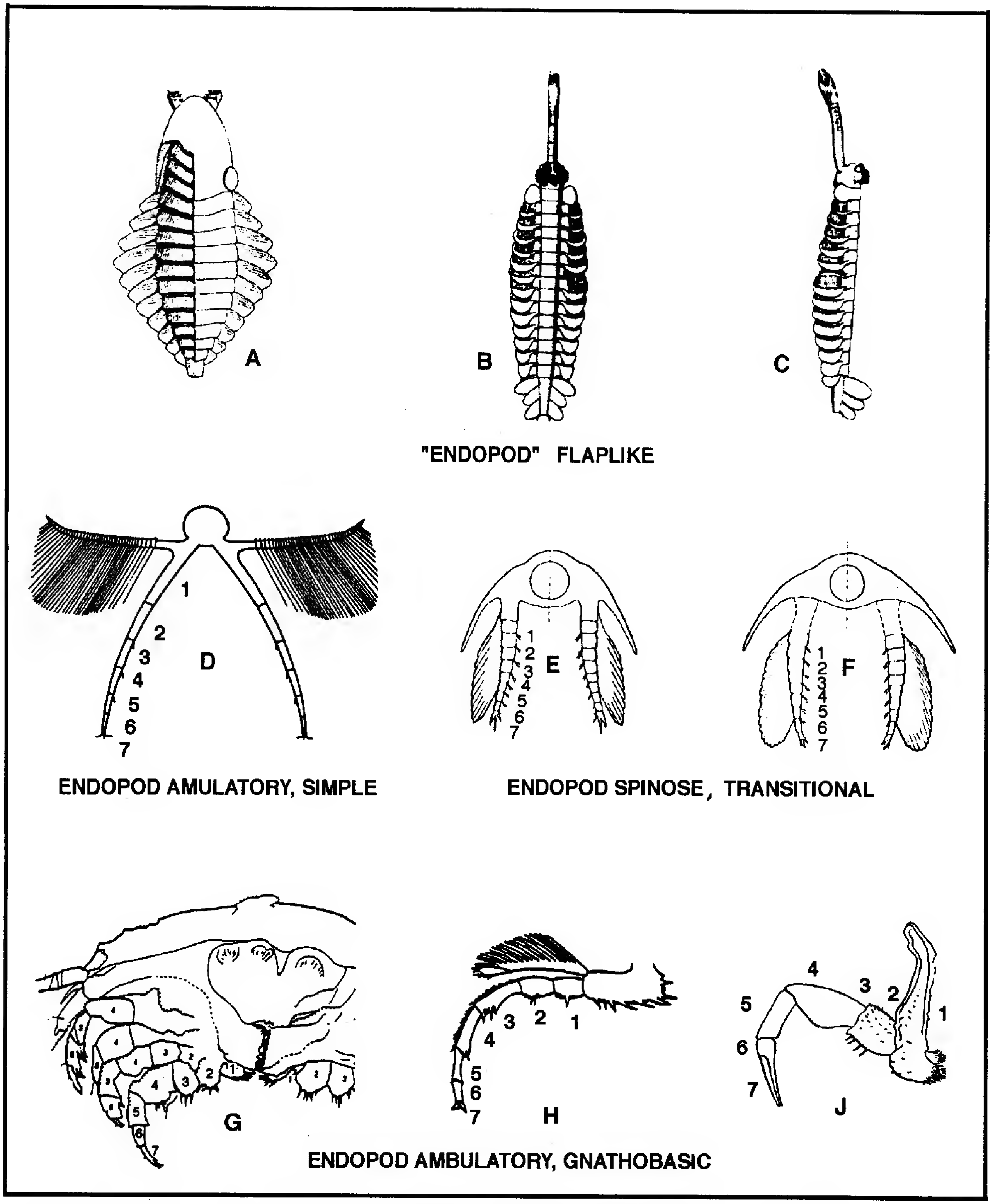


FIG. 2. BILOBATE AND BIRAMOUS POST-ORAL (HEAD AND TRUNK) LIMBS OF PRIMITIVE ARTHROPODS OF THE EARLY PALEOZOIC ERA.
A. ***Anomalocaris*** **(section) B.** ***Opabinia*** **(dorsal) C.** ***Opabinia*** **(lateral)**
D. ***Marrella*****(trunk section) E.** ***Leanchoilia*** **(post-oral section) F.** ***L.*****(trunk section)**
G. ***Sidneyia*** **(post-oral section) H.** ***Triarthrus*** **(trunk limb) J.** ***Limulus*** **(leg 2)**

but apparently lacking in those of the relatively short-bodied and more advanced *Yohoia*. Trunk limb exopods were broad, as in the trilobitomorph *Leanchoilia* (Fig. 2E, F), and margins setose, as in *Sanctacaris* (Fig. 6). At least the first pair, and possibly up to 10 pairs, of anterior trunk limbs bore a cylindrical ambulatory endopod.

Within the primitive transitional trilobitomorphs, including the Leanchoiliidacea and Actaeida (Figs. 2E, F), the 3 pairs of post-oral head limbs, and all trunk limbs, developed strong spines on the inner margins of the segments of the endopod. The spines were presumably used in grasping and holding prey organisms, much in the manner of the thoracic leg spines of eusirid amphipods and adult dragonflies. In more advanced groups of trilobitoids, the post-oral limbs of head and trunk became fully gnathobasic, in which strong teeth or spinose processes developed on the proximal (coxal and basal segments) of the endopod. The distal claws of the endopods functioned in seizing, and the gnathobases in killing and masticating, prey items prior to transfer to the mouth proper. In *Sidneyia* (Fig. 5D), the head lacked post-oral limbs but the anterior four pair of trunk limbs were strongly gnathobasic and uniramous, the remaining trunk limbs biramous. In Burgessiida and in the Trilobita proper (Fig. 2H), the 3 pairs of post-oral head limbs remained fully biramous and multifunctional. The outer ramus bore numerous respiratory lamellar spines. In the Emeraldellida, including *Emeraldella* (Figs. 6E, 7M) and *Sanctacaris* (Figs. 6, 7L) the anterior two trunk segments became fused to the head, resulting in 5 pairs of post-oral head appendages. As the locomotory and respiratory functions decreased and raptorial and masticatory functions of the head limbs increased, the endopods became more powerfully raptorial and gnathobasic, whereas the exopods became vestigial, as in *Sanctacaris*. In the aquatic chelicerates, the merostomes (e.g. *Limulus*, Fig. 2J), the head region similarly bear five pairs of strongly gnathobasic, ambulatory and essentially uniramous limbs. However, the pre-oral limbs of merostomes are chelicerate, not filamentous, and derived from very different ancestral uniantennates (see page 12). In all but the most primitive aquatic merostomes, the trunk endopods lost their ambulatory function and disappeared, whereas the anterior pairs of trunk exopods remained functional in the form of book gills and, in terrestrial derivatives, book lungs.

In the above evolutionary sequences, the development of gnathobasic limbs may have been a consequence of improved efficiency in exploiting, as food, hard-shelled prey living in soft bottom sediments. The feeding style of *Limulus* still follows this original primitive pattern.

Evolution of Food-Gathering Appendages

Within uniantennate arthropods, the morphological and functional forms of pre-oral food-gathering and food-sensing appendages may be linked in possible evolutionary pathways (Fig. 3). The presumed ancestral form of this cephalopod-style food-gathering mechanism is the large multi-segmented raptoral form typical of species of *Anomalocaris* (Figs. 3A, D). Despite anomalies of fossil limb preservation, the primary plane of motion is presumed to be essentially vertical. The paired limbs combined, nearly in parallel, to form a raptorial basket in which prey organs were captured and killed by the daggerlike posterior (inner) marginal spines (Collins, 1987). The food items were then transferred posteriorly, by deflexion and retraction of limbs, to the masticatory buccopharyngeal teeth of the mouth region. This plane of action contrasts with the nearly horizontal or oblique position of the natatory trunk limbs or lateral lobes of epi-benthic animals. In benthic species, in which the endopods of post-oral head and trunk limbs were mainly ambulatory and vertical in position, the pre-oral appendages were essentially co-planal. In *"Laggania"*-like animals (Table I - *A. nathorsti* group), with 11-segmented limbs, the posterior marginal spines were exceptionally long and strong, as if utilized in raking or digging in soft sediments (Fig. 3D).

If the plane of action is rotated to the horizontal, the paired limb spines come into opposition as a prey-capturing and killing mechanism. In this manner, and through prolongation of the head region into a long flexible annulated proboscis, the terminal raptorial claw of the free-swimming *Opabinia* can be derived (Fig. 3B; Bousfield & Collins, in preparation). The paired spines on each side are 14 in number, as in *Anomalocaris canadensis*. The distal five of these are longer and more steeply oblique and probably served in prey capture, whereas the proximal nine pairs are stouter, shorter, and more perpendicular and may have served in holding, crushing, and possibly preliminary mastication. The form and function of the claw is analogous to a modern pair of pliers. However, it was probably activated by a combination of muscular and hydrodynamic processes. The transfer of food material rearwards to the mouth by the proboscis was probably similar to the action of an elephant's flexible trunk. The proboscis does not contain the anterior gut, as proposed by Sharov (1966) (per Callahan, 1979).

In a much more highly modified Upper Carboniferous, internally segmented, squidlike counterpart, *Tullimonstrum gregarium*, described in detail by Johnson & Richardson, 1969 (Fig. 7C.2), the terminal claw was more slender, and the spines, 13-14 in number on each side, were minute (Fig. 3C). Prey items were probably small and soft-bodied, possibly free-swimming plankters, or worms or insect larvae extracted from tubes in soft bottom sediments.

In a Lower Cambrian benthic species, *Cassubia infracambriensis* (Lendzion, 1975), the number of pre-oral limb segments was reduced to 7, and segments 2-5 had large medial spinose processes (Fig. 3E). Regrettably, the plane of motion is not precisely determinable from the single incomplete fossil specimen.

In a direction presumably leading to the chelicerates, the pre-oral appendage of the protochelicerates *Jianfengia* and *Yohoia* was reduced to 3-4 segments, the outermost being double-spined and movably pincering upon the inner marginal spine of segment 2 (Fig. 3F). Limb orientation was in a vertical plane and the movable distal spine had been

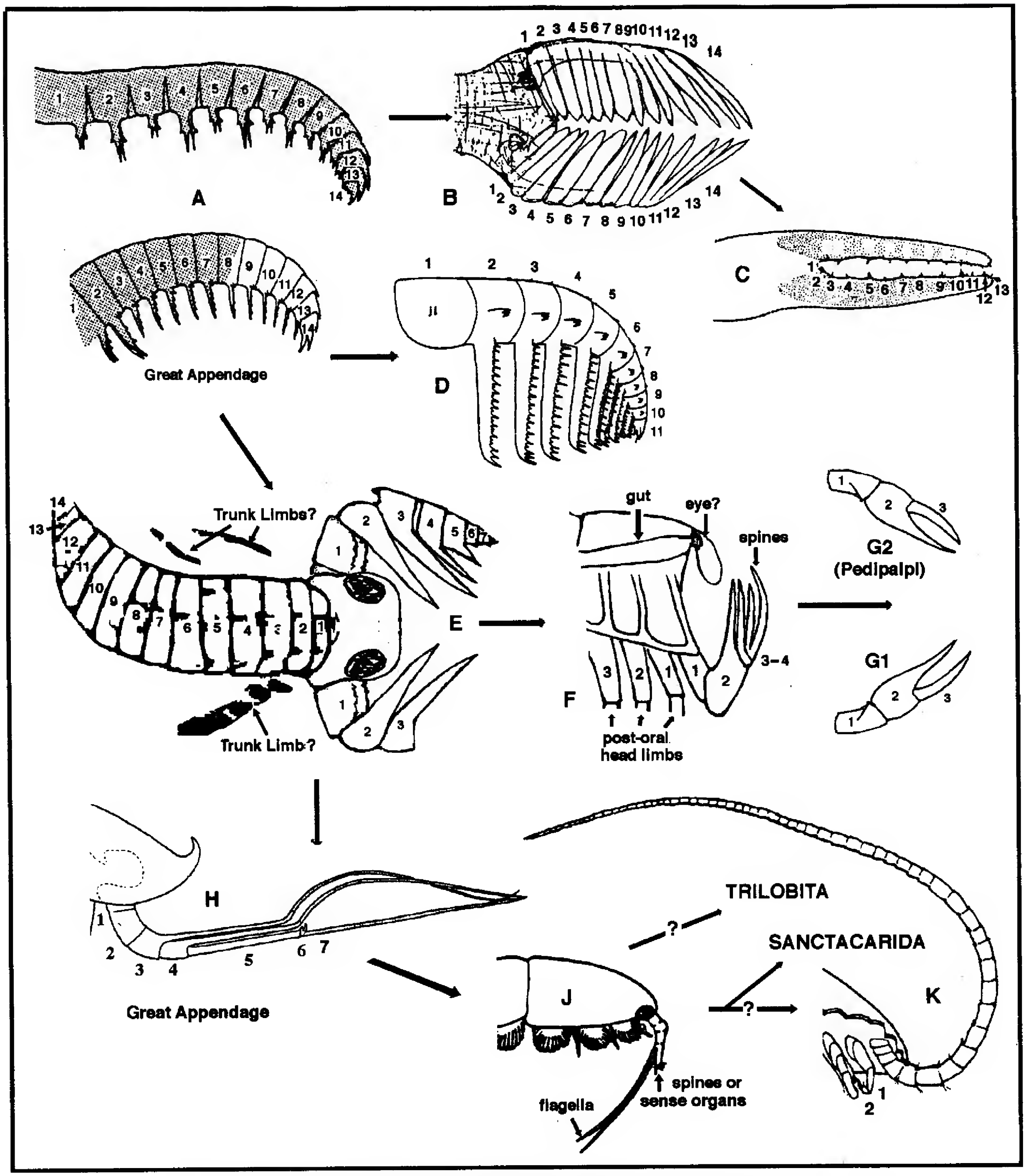


FIG. 3. PLAUSIBLE EVOLUTIONARY SCENARIOS IN THE PRE-ORAL APPENDAGE OF UNIANTENNATE ARTHROPODS (from Gould (1989) and various sources)
A. D. *Anomalocaris* spp. (Hypothetical Ancestral type)
Raptorial proboscoid line B. *Opabinia* C. *Tullimonstrum* (Carboniferous)
Raptorial chelicerate line E. *Cassubia* F. *Yohoia tenuis* G1. *Limulus* (late Palaeozoic)
Sensory flagellar line H. *Leanchoilia* J. *Actaeus* K. *Emeraldella*

rotated to the lower or inner side, as in limuloids and phalangiate arachnids (Fig. 3G1). In eurypterids, scorpions, and pedipalpate arachnids (including spiders), however, the moveable segment is on the upper or outer side of the limb (Fig. 3G2). A major link in the presumed lineage from *Yohoia* to merostomatid arachnids is not confirmed from the fossil record, viz., a yohoiid-like pre-oral appendage on a broadened head of 5 post-oral segments.

A further evolutionary thrust of the pre-oral uniantennate limb resulted in a filamentous sensory flagellum, represented in early stages by the form of the 7-segmented "great appendage" of *Leanchoilia* (Fig. 3H). The inner marginal

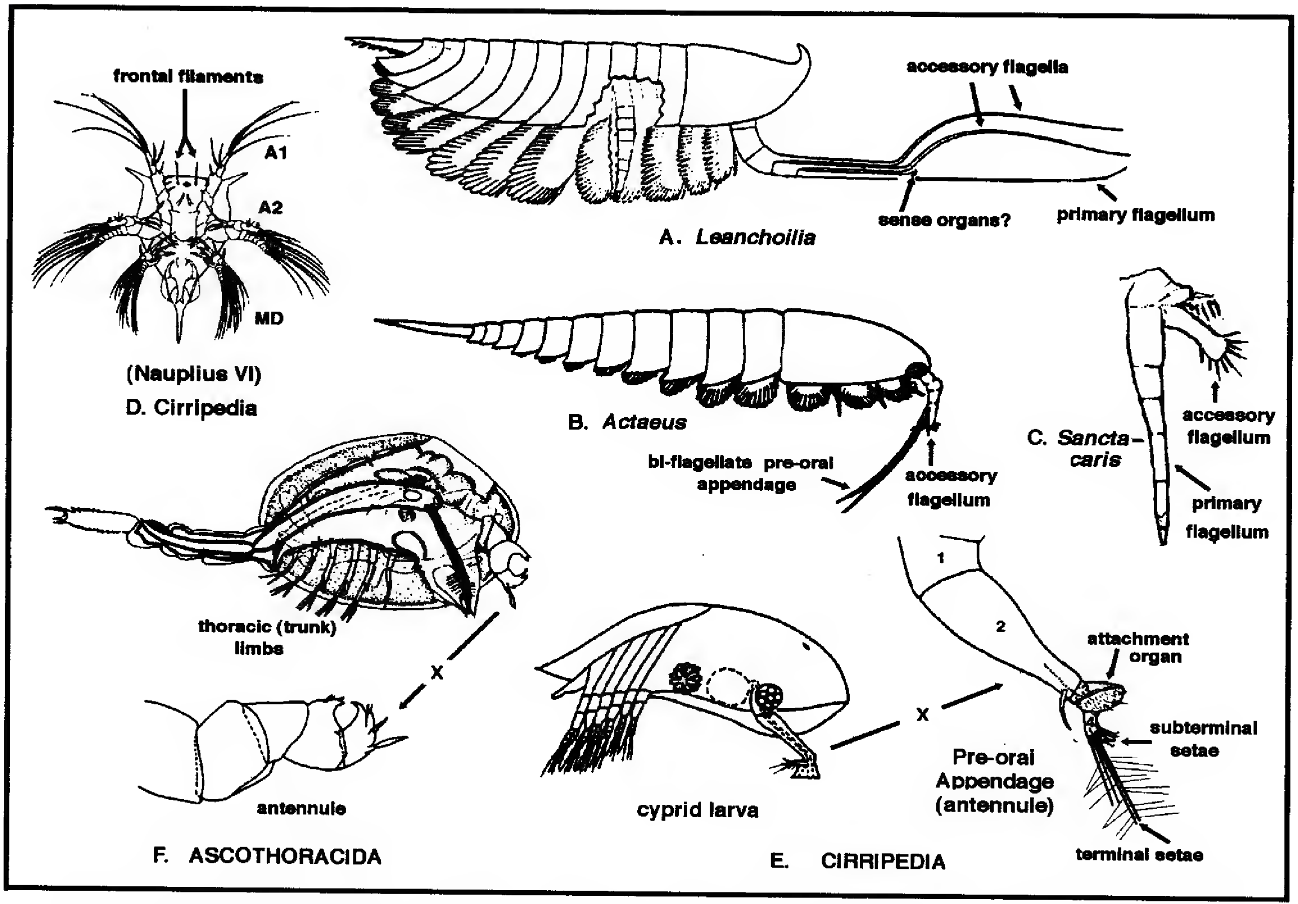


FIG. 4. PROPOSED HOMOLOGIES BETWEEN PRE-ORAL APPENDAGES OF MIDDLE CAMBRIAN TRILOBITOMORPH UNIANTENNATES AND ANTENNULES OF CRUSTACEAN (CIRRIPEDE AND ASCOTHORACID) BIANTENNATE ARTHROPODS (A,B,C after Gould, 1989; D, E, F after Schram, 1986)

spines of segments 3-4 and the terminal spine of segment 7 were apparently modified as a multi-segmented whip-like flagellum, whereas those of segments 5 and 6 were reduced to short stubs. In *Actaeus* (Fig. 7E.3), segments 3 and 4 remained flagellated, but 5-7 were much shortened, and bore short spine-like processes. In *Sanctacaris*, segment 3 (?) was short-flagellate and (4?) 5-7 terminated in a star-like cluster of spines (Fig. 4C; 6D). Derivation of a 3-segmented chelicera from such an appendage would seem improbable. The simple elongate flagellar state is attained in *Alalcomeneus* (Fig. 7E.4), *Emeraldella* (Fig. 3K) and in most other trilobitoids, including the Burgessiida and the Trilobita (Fig. 5E, F).

This analysis concludes that, in some evolutionary lines within uniantennate arthropods, the pre-oral appendage was initially a raptorial food gathering apparatus that secondarily became flagelliform. These morphotypes, including the trilobites, did not persist beyond the Paleozoic Era. In the evolution of primitive merostomes (e.g. *Chasmataspis*), a filiform antenna is unlikely to have disappeared, and a cheliform appendage suddenly appeared, as Bergström (1979) proposed for early chelicerates. The pre-oral appendage was already semi-cheliform in the proposed ancestral *Yohoia*. The trend from raptorial to sensory flagellar condition within the Trilobitoidea, rather than the reverse, is accompanied by parallel evolutionary trends in cephalization of the head, gnathobasic development of ambulatory limbs, rearward shift of respiratory limbs, and in other major character states within component major sub-taxa (p. 22).

Within biantennate arthropods, however, the evolutionary picture is different. As revealed by the limited early fossil record, and the ontogeny of larval stages of extant and fossil forms, the pre-oral appendage appears to been filiform thoughout, with few exceptions, as noted on page 14). The flagellate form has also persisted, with little change, in the myriapod and hexapod taxa that have dominated terrestrial environments since the close of the Paleozoic Era (Delle Cave & Simonetta, 1991).

Possible Homologies in Pre-oral Appendages of Uniantennate and Biantennate Arthropods.

As noted above, the significance of the first pre-oral appendage as a mechanism of food detection, food gathering, and general feeding style is basic in the Arthropoda. Both the organelles of the acron (e. g., frontal filaments, naupliar eyes) and the pre-oral first segmented head appendage are presumed sensors of environmental conditions and food sources. In uniantennates, the primary role of the latter was food gathering, a raptorial function that was retained in the single successful line of uniantennate evolution, the Chelicerata. In the biantennates, however, the appendage was primarily sensory, at an early stage, and remained so throughout evolutionary history of all major subgroups. A comparison of pre-oral limbs of selected primitive morphotypes of both uni- and bi-antennates is pertinent (Fig. 4).

In the primitive trilobitomorphs, the pre-oral appendage passes through several stages of reduction of accessory flagella and sensory organelles (Figs. 4A, B, C). leading to the simple elongate flagellar condition of the Trilobita and Emeraldellida. In a few primitive maxillopodan crustaceans with specialized life styles, however, the appendages developed correspondingly specialized sensory and raptorial functions. In cirripedes, the antennules are natatory in naupliar and metanaupliar larvae (Fig. 4D), but become organs of site selection and attachment in the cyprid larvae of sessile, shell-burrowing and parasitic forms, the Thoracica, Acrothoracica, and Rhizocephalia respectively (Glenner & Hoeg, 1995)(Fig. 4E). These 4-segmented antennules bear a perhaps superficial but remarkable similarity, and almost certainly homologous relationship to, the pre-oral appendage of the primitive trilobitoid uniantennates, *Actaeus* (Fig. 4B), and *Sanctacaris* (Fig. 4C).

However, in the ascothoracidan biantennates, parasitic on echinoderm and anthozoan coelenterates, the antennule is raptorial in the cyprid and adult stages (Fig. 4F). The terminal two segments of the 4-segmented appendage, reminiscent of *Yohoia* (Fig. 3F), form a subchela for attachment to the host, or removal of pieces of the host tissue as food.

Perhaps a more precise concept of the pre-oral appendages of long extinct uniantennates of the Cambrian Period might be derived through closer study of the antennules of these very primitive extant crustacean biantennates.

The Pre-oral Appendage of Trilobitoid Uniantennates.

The general external morphology of selected trilobitomorph uniantennates is shown in Fig. 5. In *Burgessia* (Fig. 5A), *Molaria* (Fig. 5B) and *Habelia* (Fig. 5C), the head comprises four segments (five somites) which, in *Burgessia*, subtends a broad carapace covering the trunk segments. The post-oral appendages are ambulatory, those of the trunk also respiratory. The trunk terminates in a spikelike telson, similar to that of the merostomatid chelicerates, and suggests a strongly benthic life style. In *Sidneyia* (Fig. 5D), the head is only 2-segmented, but the anterior four trunk segments bear uniramous, powerfully gnathobasic limbs that are effectively part of the cephalic masticatory complex. The posterior 3 trunk segments are free and bear a broad, flabellate telson, evidence that *Sidneyia* was a powerfully swimming benthic and epibenthic predator.

In the trilobites, [e.g., *Naraoia* , a "soft trilobite" (Fig. 5E), and *Olenoides,* a primitive true trilobite (Fig. 5F)], the head is also 4- segmented, with 3 pairs of post-oral ambulatory, respiratory, and masticatory head limbs, and 11+ pairs of similar trunk limbs. However, trilobites differ from Burgessiida in having a broad depressed head shield and trunk, the latter ending in a short pygidium or tail region of a variable number of segments. Both groups represent middle stages in cephalization of anterior trunk limbs.

Sanctacaris

On the basis of five well-preserved specimens from the Stephen Formation, near to but slightly younger than the Burgess Shale quarry, Briggs and Collins (1988) described a large carnivorous arthropod, *Sanctacaris uncata*, that they assigned to subphylum Chelicerata (Fig. 6). The broad head bears large eyes and six pairs of biramous appendages, the first five of which form a raptorial array of segmented, spinose and gnathobasic endopods with simple short antennalike exopods. The outer ramus of the sixth limb is also filamentous, but the inner ramus is short, terminating in a fringe of starlike radiating spines. The mouth is located anteriorly, presumably in a narrow gap between the first limb bases. The broad trunk is 11-segmented, the posterior bearing a paddle-shaped telson, the anterior 10 each bearing paired biramous limbs of which the exopod is large, flabellate, and natatory-respiratory in function. The inner ramus is slender, multi-segmented, and presumably ambulatory; marginal spines and/or gnathobases were not demonstrable.

However, another interpretation is utilized here. The biramous "sixth" appendage (Fig. 6D), bears a striking resemblance to the "transitional" pre-oral limb of *Actaeus,* with its star-shaped accessory flagellum (Fig. 5B), but unlike the raptorial condition in Yohoiida (Fig. 3F; 7D) or the chelicerate condition in arachnids (Fig. 6F). Furthermore it arises near the eye, in a typically pre-oral position. The five pairs of raptorial head limbs of *Sanctacaris* have apparently been displaced forward beneath the head to form a raptorial "basket", immediately beneath the mouth. These limbs, although non-ambulatory, appear to be homologous with the five pairs of post-oral head limbs of *Emeraldella* (Fig. 6E). The latter has a single filamentous pre-oral flagellum that is apparently homologous with the short biramous "antenna" of *Sanctacaris.* In *Emeraldella* also, the post-oral head limbs are similar to the trunk limbs in being strongly ambulatory as well as gnathobasic.

On this interpretation, and in agreement with Delle Cave & Simonetta (1991), *Sanctacaris* is removed from the Chelicerata and placed in Class Emeraldellacea within the revised superclass Trilobitoidea (Table III, p. 24). *Sanctacaris* thus stands as a unique, relatively advanced, but apparently short-lived, sideline of Cambrian uniantennate evolution.

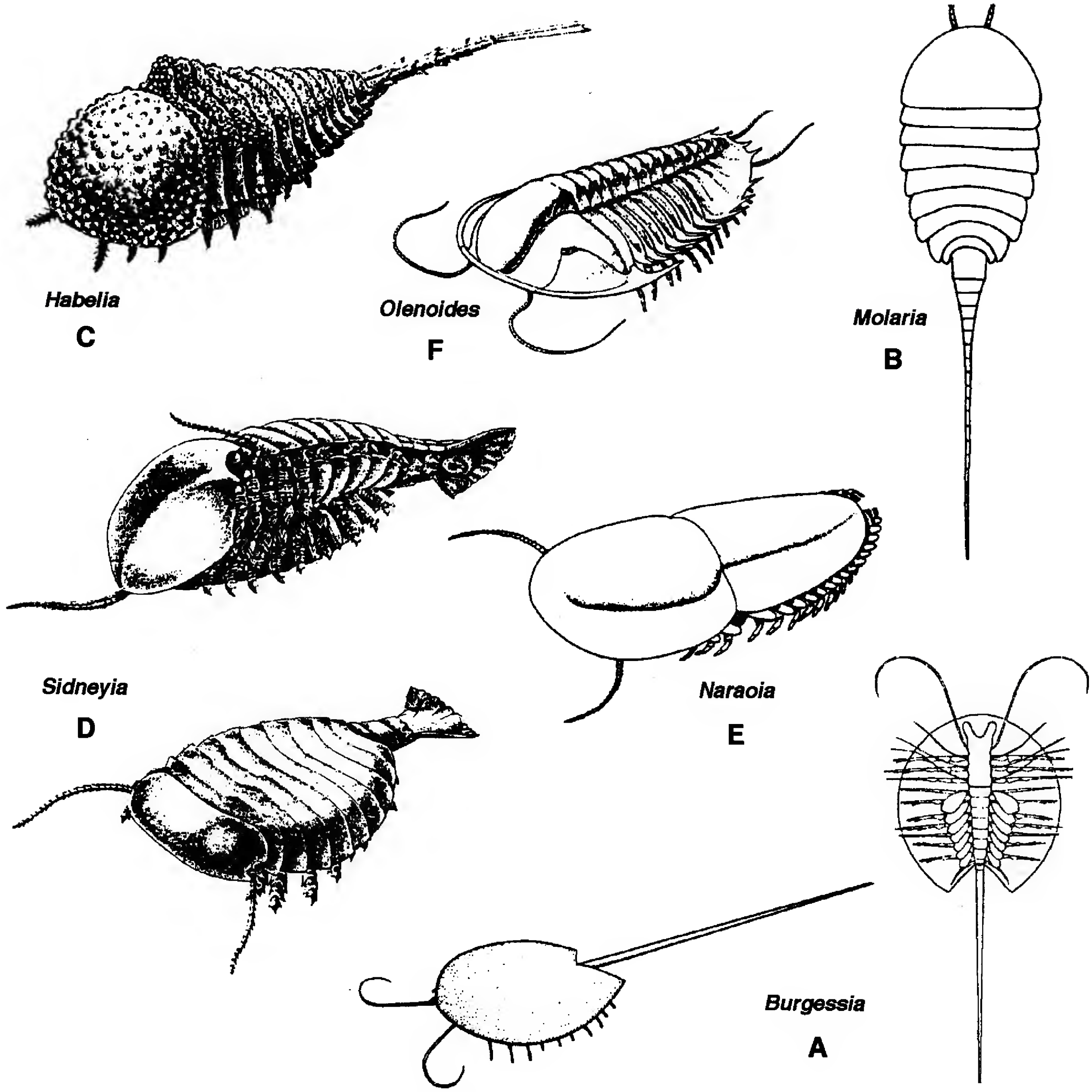


FIG. 5. CAMBRIAN ARTHROPODS: WITH GNATHOBASIC LIMBS AND FILAMENTOUS PRE-ORAL APPENDAGES (variously from Gould (1989) and Briggs et al (1993)

Evolutionary Pathways in Uniantennate Arthropods

Plausible evolutionary pathways within uniantennate arthropods of the Cambrian period that led to more highly evolved trilobitoid and chelicerate faunas of the middle and late Paleozoic are summarized in Fig. 7 (p. 17). The chart embodies information provided in Table I, and figures 2, 3, 5 & 6 especially. The degree of morphological evolution and specialization of feeding style is represented by four blocks or zones, proceeding along the X-axis, from the most primitive (pharyngeal feeding) on the left, through a narrow transitional band in the middle, to limb gnathobasic and limb masticatory feeding types on the right. Of these, the chelicerate form on the extreme upper right is the most advanced. The Y-axis represents a generalized, rather than definitive, time scale.

As noted previously, the most primitive and presumably ancestral uniantennate arthropod of the late Precambrian, Vendian, and Early Cambrian Periods was a member of the predatory and pharyngeal-feeding Anomalocarida, illustrated on the lower left. These large-eyed animals possessed a short head (2-4 somites), and a multisegmented body with bilobate lateral pleurae or biramous ambulatory and respiratory paired appendages. In a cephalopodlike feeding

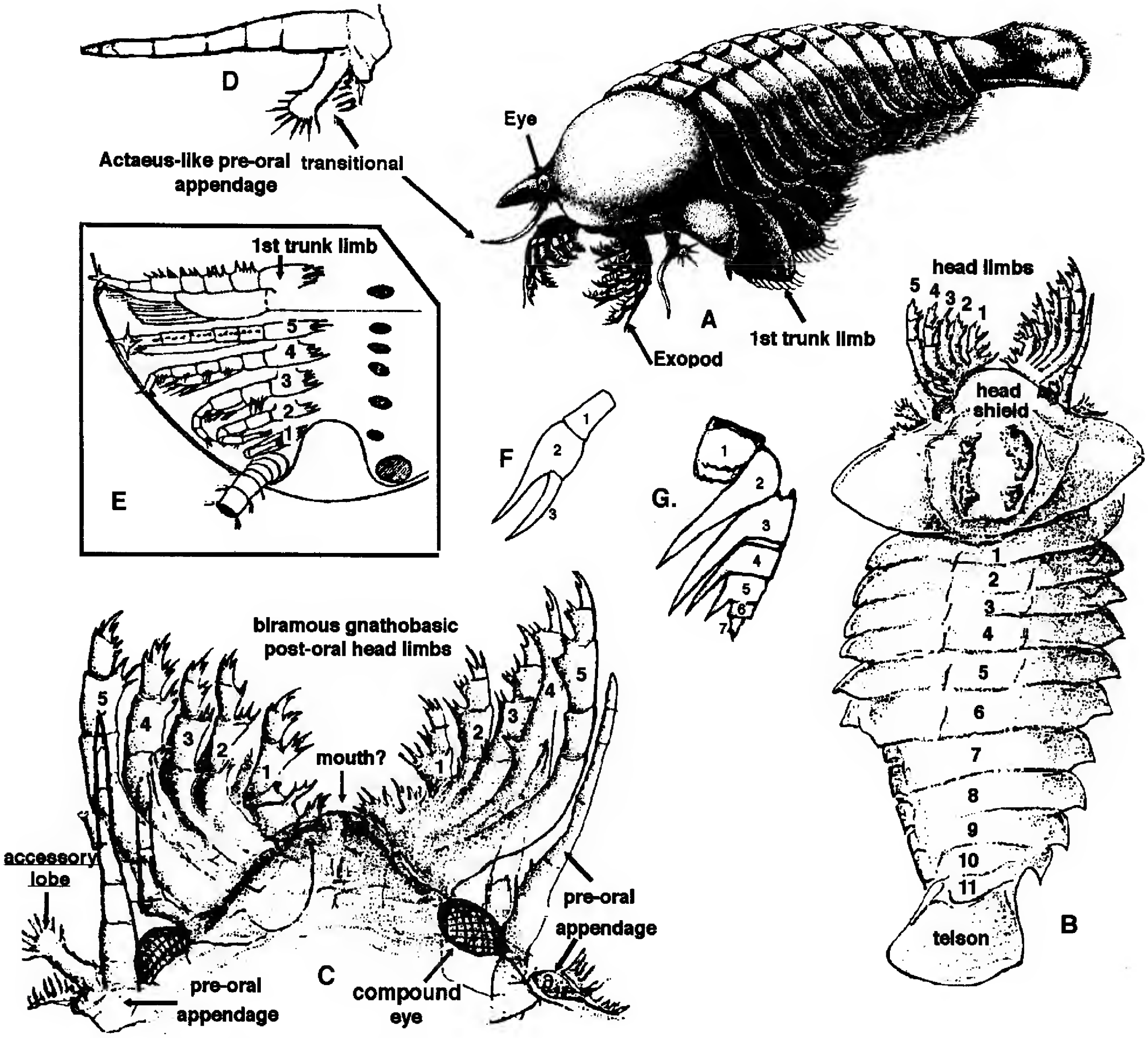


FIG. 6. EXTERNAL MORPHOLOGY OF *SANCTACARIS* (modified from Briggs & Collins, 1988) A. Life-like Reconstruction. B. Dorsal View. C. Head region (MAG. X), D. Pre-oral appendage (X) E. (Inset). Head appendages of *Emeraldella* (ventral view) F. *Limulus* Left chelicera G. *Cassubia* Left Pre-oral Appendage.

style, paired raptorial pre-oral head appendages apparently captured and transported food to the mouth region where it was masticated and ingested without post-oral limb assistance. Within the Anomalocarida per se, development of a benthic life style was accompanied by reduced segmentation but stronger armature, possibly partly fossorial in function, of the pre-oral raptorial limbs (e.g., in *"Laggania"* - type fossils (Table I) and in *Cassubia* Lendzion, 1977, centre line).

Of the three proposed evolutionary offshots from the Anomalocarida, the epibenthic probosciferidans (on the left) developed a very specialized food capturing mechanism, similar in function to the hetercotyl arms of cephalopods, but found nowhere else among the arthropods. It consisted of horizontally opposing limbs fused together in a claw-like appendage that was activated by a flexible proboscoid extension of the anterior head region. Its movements were presumably triangulated and co-ordinated by widely set pairs of stalked compound eyes. The small size of this "proboscis", and lack of peribuccal or pharyngeal teeth, indicate that the prey organisms were very probably small and soft-bodied.

Cladistic presentation of relationships of *Tullimonstrum* by Beall (1991) may be a case of "bending the facts" to fit theoretical models. None of his cladograms provides close relationships between *Tullimonstrum* and other major invertebrate groups, and each cladogram contradicts relationships depicted by the others. The "re-interpreted" animal appears unfunctional (e. g., a vertical tail on a depressed trunk) and inconsistent with the taxonomic details of Richardson (1966) and Johnson & Richardson (1969) that resulted

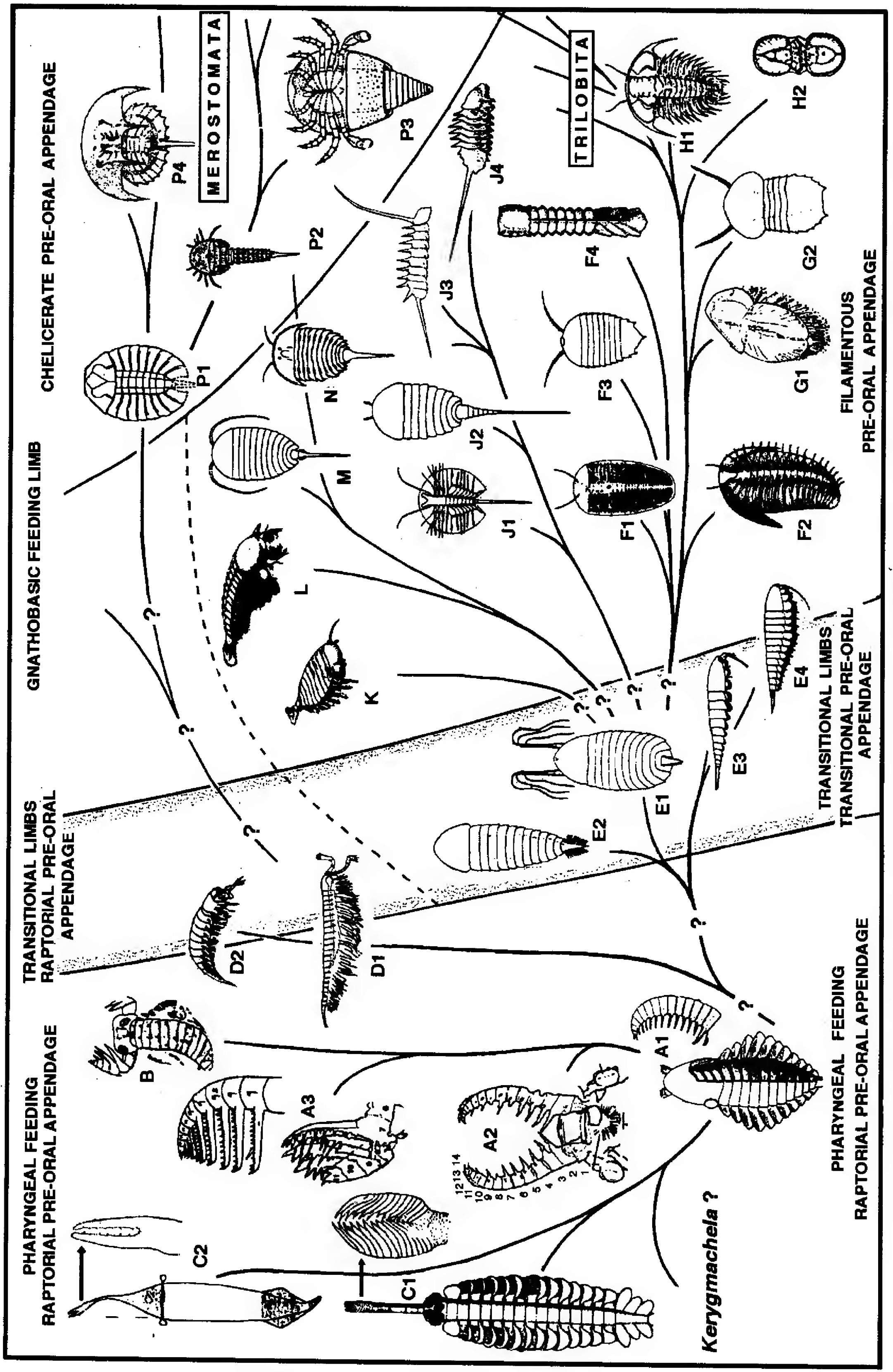


FIG. 7. RELATIONSHIPS OF CAMBRIAN UNIANTENNATE ATHROPODS BASED ON FEEDING MECHANISMS

A1. *Anomalocaris canadensis* A2. *Anomalocaris sp (Chengjiang)* A3. *Anomalocaris nathorsti* B. *Cassubia* C1. *Opabinia* C2. *Tullimonstrum*! D1. *Jianfengia* D2. *Yohoia* E1. *Leanchoilia* E2. *Acanthomeridion* E3. *Actaeus* E4. *Alalcomenaeus* F1. *Nathorstia* F2. *Tegopelte* F3. *Kumaia* F4. *Mollisonia* G1. *Naraoia* G2. *Liwia* H1. *Olenoides* H2. *Agnosta* J1. *Burgessia* J2. *Molaria* J3. *Economocaris* J4. *Thelxiope* K. *Sidneyia* L. *Sanctacaris* M. *Emeraldella* N. *Aglaspis* P1. *Triopus** P2. *Chasmataspis* P3. *Diploaspis*+ P4. *Euproops*+

*L. Ordovician +Devonian !Carboniferous

FIG. 7. RELATIONSHIPS OF CAMBRIAN UNIANTENNATE ATHROPODS BASED ON FEEDING MECHANISMS

from careful observations on numerous specimens.

A more successful evolutionary experiment typifies the mostly benthic trilobitoid line to the right. In it, the pre-oral limb lost its raptorial function and became flagelliform, multi-segmented, and presumably mainly sensory and perhaps tactile in function. Simultaneously, the post-oral head and trunk limbs developed a linear gnathobasic endopod which, through various degrees of cephalization of anterior trunk segments, formed a masticatory feeding field of 2-5 pairs of post-oral head appendages. Remarkably, the species of Leanchoiliidea (including *Acanthomeridion* from Chengjiang deposits) sit squarely in the transitional zone of both pre- and post-oral limb evolution. *Alalcomenaeus,* having the most advanced, mono-filamentous pre-oral appendage, also has nearly fully gnathobasic post-oral appendages (Delle Cave & Simonetta, 1991).

Of the flagellated trilobitoids with 3 post-oral head segments, the "spike-telsonic" group (centre right) encompassed the *Habelia* subgroup having armoured processiferous bodies and short antenna. The associated *Molaria,* also having filamentous antenna and only three post-oral head segments, is an unlikely precursors of the chelicerates, as proposed by Delle Cave and Simonetta (1991, Chart II). Trilobitoideans with pygidial (non telsonic) abdomens (lower right) included narrow-bodied "idotheid" or "asellid" isopod-like forms such as *Mollisonia* and *Urokodia* that may have occupied algal substrates. They also included broad, flat-bodied, fossorial types with protective exoskeletal armour, leading to their only successful subgroup, the trilobites, that diversed in the later Paleozoic times.

The trilobitoids include the Emeraldellidacea that have 5 post-oral head segments and a spike-like telson (upper right). The group here includes the aglaspids, thought to possess chelicerae prior to the work of Briggs et al (1978). Aglaspids "straddle" the Upper Cambrian- Lower Ordovician boundary. The Devonian *Cheloniellon* may be a distant descendent of the main line of Emeraldellidea. As mentioned above, a carnivorous form with paddle-like telson, *Sanctacaris,* is considered an early offshoot of this same line. This species has 5 distinct post-oral head segments, each with biramous paired raptorial limbs. *Sidneyia* has no post-oral head limbs but the first four trunk limbs are uniramous (lacking gills), strongly gnathobasic and form, effectively, a post-oral masticatory field of four segments. *Sidneyia* is here regarded as a very early (relict) stage of cephalization of anterior trunk appendages, and had a separate origin (Fig. 7K).

The most successful anomalocarid offshoot is here believed to be the *Jianfengia-Yohoia* line, to the upper right of Fig. 7. The post-oral head limbs, in the process of losing respiratory exopods, were already ambulatory and transitional in form. Although the pre-oral head limbs remained raptorial, their reduced size and segmentation and subcheliform appearance are plausible precursors to the fully chelicerate condition found in the most primitive arachnids, the merostomes, of the Lower Ordovician (upper right). However, the viability of this proposed evolutionary connection awaits discovery of a broadly flat-bodied fossil having transitional masticatory post-oral head and trunk limbs and a more clearly cheliform (rather than geniculate) pre-oral appendage. *Triopus* (Fig. 7P.1) may approach that predicted form but its appendages are poorly known. *Chasmataspis* (Fig. 7P2) is the most primitive Lower Ordovician undoubted chelicerate, leading to the eurypterids. Although not completely understood (Bergström, 1979), *Chasmataspis* has 5 post-oral head segments and 12 trunk segments. The total is one more than the combined number of post-oral segments of the presumed ancestral *Yohoia.*

The Euthycarcinoidea Enigma

The enigmatic group of aquatic arthropods classified as Euthycarcinoidea, is based on a half-dozen limnic (?) species that existed from Carboniferous to Triassic time. Bergström (1979) summarized information on the Triassic genera *Euthycarcinus* and *Synaustrus,* and Schram and Emerson (1991) utilized the upper Carboniferous genera *Pieckoxerxes* and *Kottixerxes* in developing their newly proposed Arthropod Pattern Theory (Fig. 8). The broad head shield is typically composed of 3 somites including an eye-bearing acron, an anterior procephalon with a single pair of filamentous antennae, and a posterior gnathocephalon bearing a set of mandible-like appendages and on which the mouth opens ventrally. The broadened trunk is divided into an anterior (thoracic) region of diplo- or triplo- segments each bearing paired uniramous limbs, and a posterior narrower and limbless abdomen that terminates in a spikelike telson.

According to Schram & Emerson (loc. cit.), the possession of uniramous limbs and diplosegments may link these animals to the ancestry of the terrestrial myriapods and hexapods (Uniramia of Manton, 1972). On the other hand, the overall appearance of euthycarcinoideans is grossly similar to some uniantennate arthropods having 3-6 head segments, and filamentous pre-oral limbs, e.g., *Leanchoilia, Habelia,* and *Emeraldella.* However, unlike the uniantennates, the trunk endopods are filamentous, multisegmented, and lack raptorial spines, gnathobases, and/or terminal claws. The leg segments bear slender posterior marginal spines that are possibly of both natatory and respiratory support function, and in that respect resemble the exopods of some uniantennate arthropods (e.g., of Trilobitoidea).

The Lower Cambrian Chengjiang fossil deposits in Yunnan region, South China, discovered in 1984, contain a number of very primitive arthropods yet imperfectly known, and mostly not included here. However, one of these, *Fuxianhuia protensa* Hou, 1987b, is remarkably similar in overall form to the euthycarcinoideans (above, and figs. 8A, 9) as detailed recently by Chen et al. (1995) (Fig. 8 A-H). The body consists of a short, broad, head shield and an elongate trunk region. The latter is divided into a thorax of 17 broad, depressed, limb-bearing segments, and an abdomen of 14 narrower and more cylindrical, legless segments, the last bearing a prominent telson spine. The head bears an anterior pair of large stalked eyes, a pair of filamentous pre-oral appendages (antennules) on somite 2 and, ventrally on

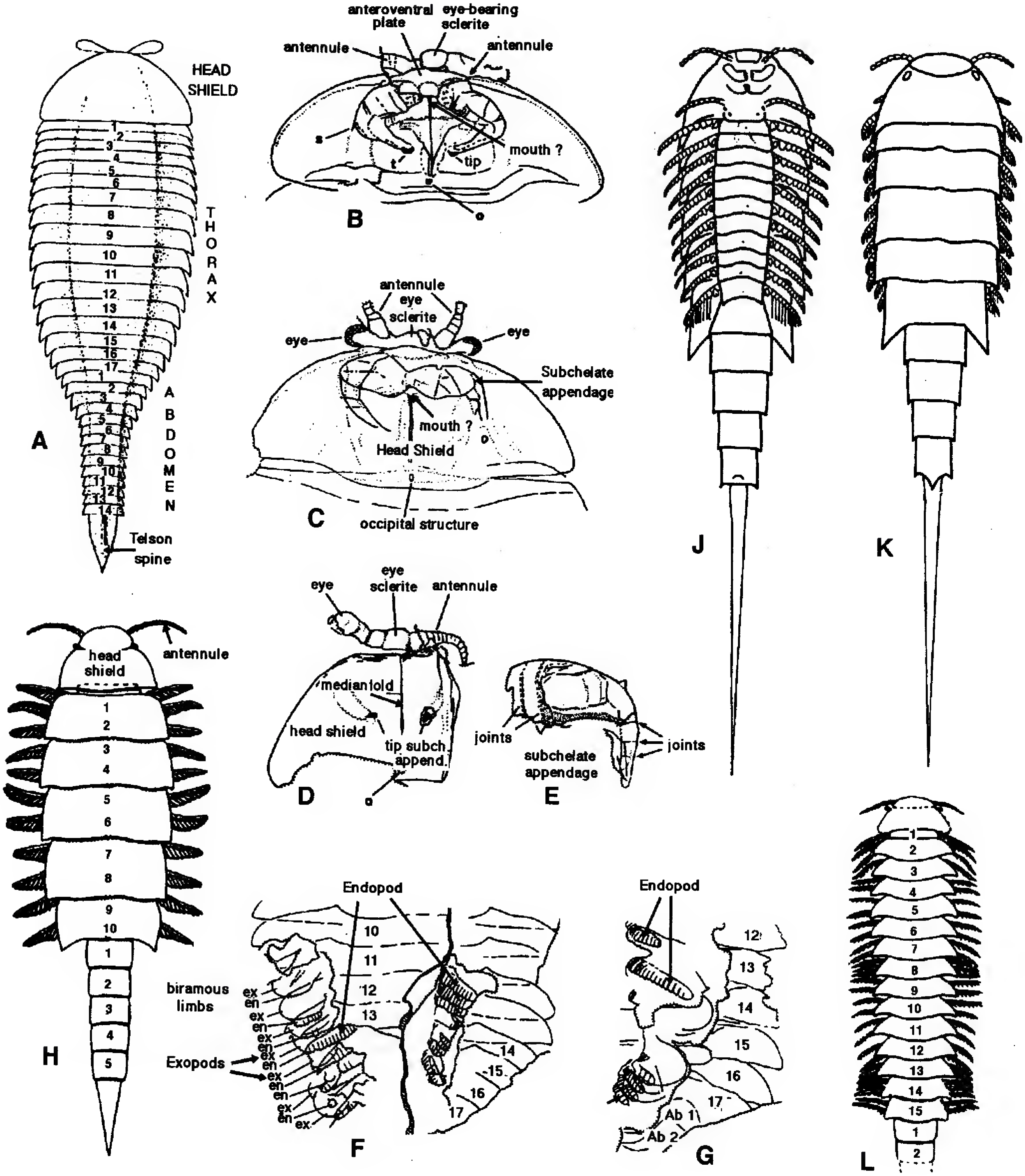


FIG. 8. **EUTHYCARCINOIDEA:** ***Fuxianhuia protensa*** **Hou, 1987 (Middle Cambrian) A. Dorsal reconstruction Head shield B., C. ventral reconstr. D. dorsal reconstr. E. Subchelate head appendage F. Abdomen, ventral G. Abdomen (ventral X. 1987; showing limbs) H.** ***Pieckoxerxes piekoae*** **K.** ***Kottixerxes gloriosus*** **(A, B - after Hou, D-G (after Chen et al, 1995) H, L. (after Schram & Emerson, 1991). J, K,** ***Euthycarcinus kessleri*** **(after Bergström, 1979).**

somite 3, a pair of subchelate raptorial limbs, presumably arising on either of side of the mouth. These superficially resemble the raptorial head limbs of the uniantennate arthropod *Cheloniellon*, the raptorial maxillae of remipede crustaceans, and the raptorial first thoracic limbs of belostomatid hemipteran insects. However, they are unlike the paired palpless mandiblelike structure of the mouth region ascribed to a few specimens of *Euthycarcinus* (Bergström, 1979).

In other details, however, the similarity of *Fuxianhuia* to euthycarcinoideans is remarkably close. The trunk limbs are biramous, with thin plate-like exopods, but the endopods are cylindrical, multisegmented, and lack terminal claws. These endopods are also similar to the multisegmented, basally shafted rami of larval skaracarids of the Cambrian "Orsten" fauna (Fig. 9, part). The limbless abdomen is found elsewhere in most maxillopodan crustaceans (e.g., several Skaracarida, Cirripedia, Copepoda, etc., and the Cephalocarida) as well as some phyllocaridans and phyllopod biantennates. The incomplete basal fusion of the trunk exopods and endopods is reminiscent of the lateral lobe-like paired flaps or limbs of the primitive dicephalosomatid uniantennates. Modern aquatic predators with "jacknife" raptorial limbs (above) are all free-swimming pelagic predators, perhaps indicating a similar life style in euthycarcinids.

In summary, *Fuxianhuia* bears some similarity to nearly every major group of arthropods of the Lower and Middle Cambrian Period but does not conform completely with any. In the very primitive structure of his head and locomotory limbs, and multi-segmented body, it is close to a model arthropod ancestral type (e.g., of Snodgrass, 1956). However, the presence of two pairs of pre-oral head limbs, the first of which is filamentous and the second raptorial, is similar to the situation in crustaceans and some phyllocaridans, and thus essentially biantennate. This feature, along with the multisegmented, clawless endopods of the thoracic region, justify its inclusion within the class Euthycarcinoidea. Its other members are of more recent geological age, but sufficiently distinct to justify erection of the primitive subclass Fuxianhuiacea (Table IV, p. 27).

Evolutionary Relationships in Aquatic Biantennates

A recapitulation of plausible evolutionary pathways within early aquatic biantennate arthropods is sketched in Fig. 9. On the left of the chart are connectives for two genera of skaracarid crustacean larval forms, a phosphotocopine ostracod, and a thecostracan cyprid, that represent the primitive evolutionary phases of skaracarid, ostracod and cirripedian maxillopodans of Cambrian times. Their primitive character states included the shaftlike form of the basal portion of the post-oral head limb endopods, the unbossed condition of their ramal spines and setae, and the multisegmented rami that are found variously in early naupliar stages of Copepoda, Cirripedia, and other extant maxillopodan crustacean subgroups. The systematics and evolutionary history of maxillopodan crustaceans are relatively well known (e.g., in Schram, 1986), and are not discussed further here.

In the centre are the euthycarcinoideans of which *Fuxianhuia* from the Lower Cambrian is here designated the the most primitive member. The Upper Carboniferous and Triassic members are shorter-bodied, with diplo- and triplotrunk segments, uniramus limbs, and may be ancestral to groups with the Myriapoda. However, further evidence from Silurian and Devonian representatives is needed to clarify such a phylogeny.

To the centre right are connectives between the three subclasses of biantennates recognized here within a revised and restricted definition of Latreille's original crustacean class Phyllopoda (p. 26). These Cambrian groups resemble extant branchiopodan and leptostracan crustaceans, at least superficially, and may have had a late Precambrian or Vendian common ancestor. The branchiocarids and odaraiatids were regarded as unique arthropods and/or crustaceans by Briggs (1976, 1981). However, they differ from true crustaceans in the 3-segmented head structure (lack of clearly defined maxillae and maxillary segments) and the carapace is mandibular rather than maxillary in origin. Although Schram (1986), following Briggs (1978), assigned the Canadaspida to Malacostracan subclass Phyllocarida, Dahl (1984, 1987) convincingly demonstrated primary differences of tagmatization, total number of body segments, position and form of the presumed mandible, limb structure and other anomalous features that, under existing definitions, remove the Canadaspida from the Phyllocarida, and the true Crustacea.

In Fig. 9, lower right, are the marrellomorphs. These represent one of the few aquatic biantennate arthropods with qualifications for direct ancestry to the myriapods and hexapods, its leg features postulated by Kukalova-Peck (1992). Thus, marrellomorphs are biantennate and the head limbs possibly mandibulate, but not ambulatory-gnathobasic. They are mainly benthic in life style and the anterior limbs are apparently double-clawed, suited to walking or crawling over firm substrates. They also possess similar body tagmatization and limb structure, and the telson is minute or lacking. The leglike maxillary and labial palps of *Dasyleptus*, an Upper Carboniferous monuran wingless insect (Fig. 9) are remarkably similar in form to the endopods of the ambulatory head limbs of the Devonian marrellomorphs *Mimetaster* and *Vachonisia* (Stürmer & Bergström, 1976). Loss of the second head segment and its antennalike pre-oral limbs in myriapods and hexapods accords with overall evolutionary trend to reduction of limbs and accessory lobes that accompany a shift from aquatic to terrestrial life style. In air, gravitational effects on limb structure are more significant; two pairs of sensory limbs would thus appear to be mechanically unwieldy and functionally unnecessary.

Phylogenetic Tree of the Arthropoda

An annotated classification of uniantennate and biantennate arthropods is presented in Tables III (p. 25) and IV (p. 27) respectively, the number of higher categories of which are summarized in Table V (p. 29). Hypothetical

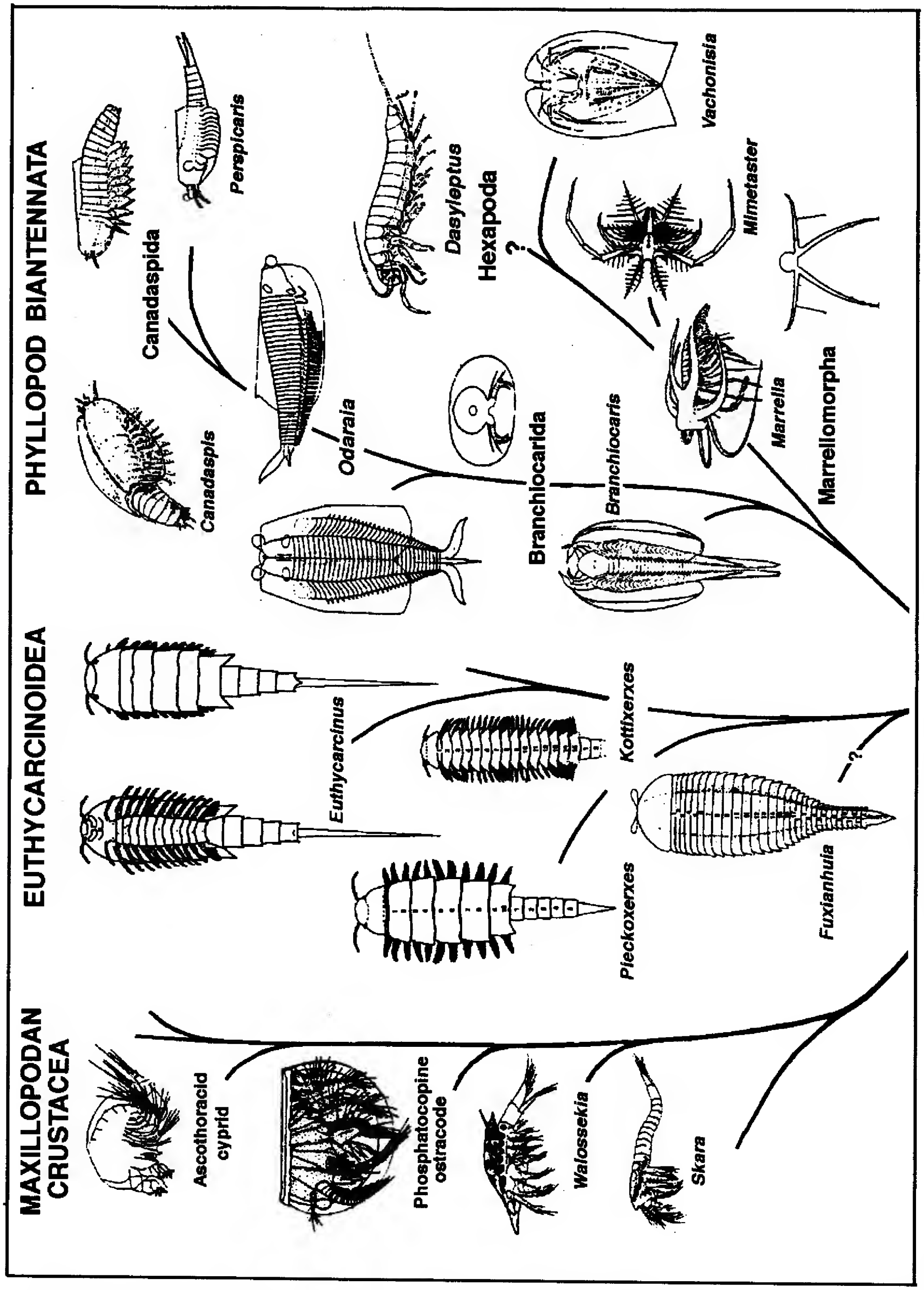


FIG. 9. PHYLETIC LINKAGES WITHIN BIANTENNATE ARTHROPODS OF THE PALEOZOIC ERA Maxillopoda - after Schram, 1986; Euthycarcinoidea - after Bergstrom, 1979; Schram & Emerson, 1991; Chen et al, 1995; Phyllopoda - after Gould, 1989; Marrellomorpha - after Bergstrom, 1979; Hexapoda - after Kukalova-Peck, 1987).

FIG. 9. PHYLETIC LINKAGES WITHIN BIANTENNATE ARTHROPODS OF THE PALEOZOIC ERA

relationships of the major genera of the Cambrian Period to each other and to other major groups of arthropods over the 600+ million year geological and evolutionary time scale are summarized in the accompanying chart (Fig. 10, p. 23).

Phyletic relationships may be presented in a number of graphical ways, including cladograms (e.g. Briggs & Fortey 1989), following an earlier attempt by Briggs (1983). Those authors (1989) utilized 26 characters and corresponding character states in deriving an arrangement in which the biantennate branchiopods clustered near the base, the trilobites at the advanced end, and various trilobitoideans and arachnids at intermediate levels of the evolutionary scale. Whereas this scheme has an overall plausibility, it is limited in detail by the omission of dicephalosomatid arthropods or other related outgroup taxon, by other possibilities in the ordering of some character states, and by weaknesses inherent in cladistic analyses generally (see Gosliner and Ghiseln, 1984).

In view of limitations of cladistic methodology at this stage of knowledge, the writer finds merit in modifications of the simple phyletic tree arrangements of Delle Cave & Simonetta (1991), for various early arthropod subgroups, as outlined here in Fig. 10. The hypothetical " tree" commences somewhere within late Precambrian times, in conformity with the views of Dzik & Krumbiegel (1989). Thus, representatives of tardigrade and onychophoran pararthropods and both uniantennate and biantennate arthropods were already present in the earliest (Lower Cambrian) fossil deposits (Dzik & Lendzion, 1988). Also, protarthropods (e.g *Xenusia*) and some antennognath arthropods (e.g., *Spriggina, Praecambridium*) are also known from Ediacrian and Vendian fossil deposits (Delle Cave & Simonetta, 1991).

The earliest and morphologically most primitive uniantennulate subgroup of Cambrian times is here considered to be the dicephalosomatids (p. 25). The primitive anomalocarids did not surive the Cambrian and the more advanced probosciferans lasted only until the Upper Carboniferous. The Yohoiida, possibly on a direct ancestral line with the chelicerates, also became extinct in the Cambrian. Not yet discovered, however, is a theoretical Cambrian fossil form having a 6-segmented head, transitional post-oral masticatory limbs, and fully cheliceriform pre-oral appendages that might directly link the group with the chasmataspids and primitive aquatic arachnids of Ordovician and later periods. Of the aquatic merostomes, the eurypterids diversified during the mid Paleozoic but became extinct prior to the Mesozoic, and a few relict limulids are the only modern survivors of those primitive aquatic chelicerates.

The Trilobitoidea embodied various combinations of head and trunk segments having filiform, sensory pre-oral appendages and raptorial, gnathobasic, post-oral feeding and ambulatory limbs. Several of these, including early trilobites (e.g., olenellids) apparently became extinct during the Cambrian, although the Emeraldellidea persisted until the Devonian (e.g., *Chelionellon*). The more advanced trilobites became the single most speciose and diverse group of aquatic uniantennates during the early Paleozoic. They apparently survived longer than any other other arthropod group having only 4 head segments, but were gone by the beginning of the Mesozoic.

The paleohistory of the biantennates is less clear. Primitive biantennates, the euthycarcinoids, marrellomorphs and phyllopods occurred, even abundantly, in the Cambrian. However, the marrellomophs survived only until the Upper Paleozoic, and the euthycarcinoids to the Triassic. As noted on page 18, the marrellomorphs provide a plausible (but not confirmed) aquatic ancestor to the terrestrial myriapods and hexapods whose fossil records commenced in the lower Devonian and upper Silurian periods. Kukalova-Peck (1992) has provided convincing evidence that the myriapod and hexapods could not have originated from the Xenusian-onycophoran line of "uniramians", a conclusion supported by the present study.

The fossil record of early crustaceans is uneven, but little doubt exists, especially as result of remarkable new micro-fossils in the Swedish 'Orsten' deposits, revealed by Walossek & Müller (1989), that the maxillopodans were a very diverse biantennate group by Middle and Upper Cambrian times. Maxillopodans continued to exploit aquatic niches and food resources in which small size, free-swimming metamorphic developmental stages, and filter-feeding mechanisms are advantageous. The somewhat larger Branchiopoda, by developing a resting egg stage, have managed to survive, mainly in temporary freshwater habitats, over a comparable time frame. Their non-palpar mandible, even in early naupliar stages (Sanders, 1963), may indicate an early link with the Phyllopoda. There is little basis for a direct phyletic link with the trilobitoideans, as studied by Hessler & Newman (1975).

With respect to the Cephalocarida and the Remipedia, crustacean classes discovered only during the later half of this century, their body and limb structures are more primitive than most other maxillopodans, and certainly the malacostracans (Schram, 1986). Despite their problematical late Paleozoic (or non-existant) fossil records, an early Paleozoic origin for both groups is a reasonable expectation.

The Malacostraca may be considered the dominant and most diverse crustacean class of Recent times (Bousfield & Conlan, 1990). Transfer of the orders Canadaspida and Branchiocarida from the Crustacea to the phyllopod Biantennata (p. 25), leaves the Upper Devonian protoglyphaeid reptantian *Palaeopalaemon newberryi* as the earliest confirmed malacostracan fossil record (Schram, 1986). However, the relatively plesiomorphic body segmentation and limb structure of the Leptostraca (*sensu strictu*), as well as the Hoplocarida and Syncarida, would suggest a somewhat earlier beginning for the malacostracans, possibly during the Silurian or late Ordovician.

THE CAMBRIAN ARTHROPOD FAUNA: EVOLUTIONARY TRENDS.

Early trends in the direction of morphological and behavioural evolution in arthropods, revealed by Burgess Shale and other Cambrian faunal assemblages, are summarized as follows:

(1) Within uniantennate arthropods, the ancestral pharyngeal and peribuccal feeding methodology was replaced by a masticatory assemblage of post-oral gnathobasic limbs of the head region. The taxonomic series of *Anomalocaris, Leanchoilia* and *Emeraldella* represents this transformational process.

(2) Also within the uniantennates, the primitively large raptorial food-gathering limbs of the pre-oral head region gave rise to short, paired cheliform and chiefly masticatory appendages within the higher (terrestrial) Chelicerata. The

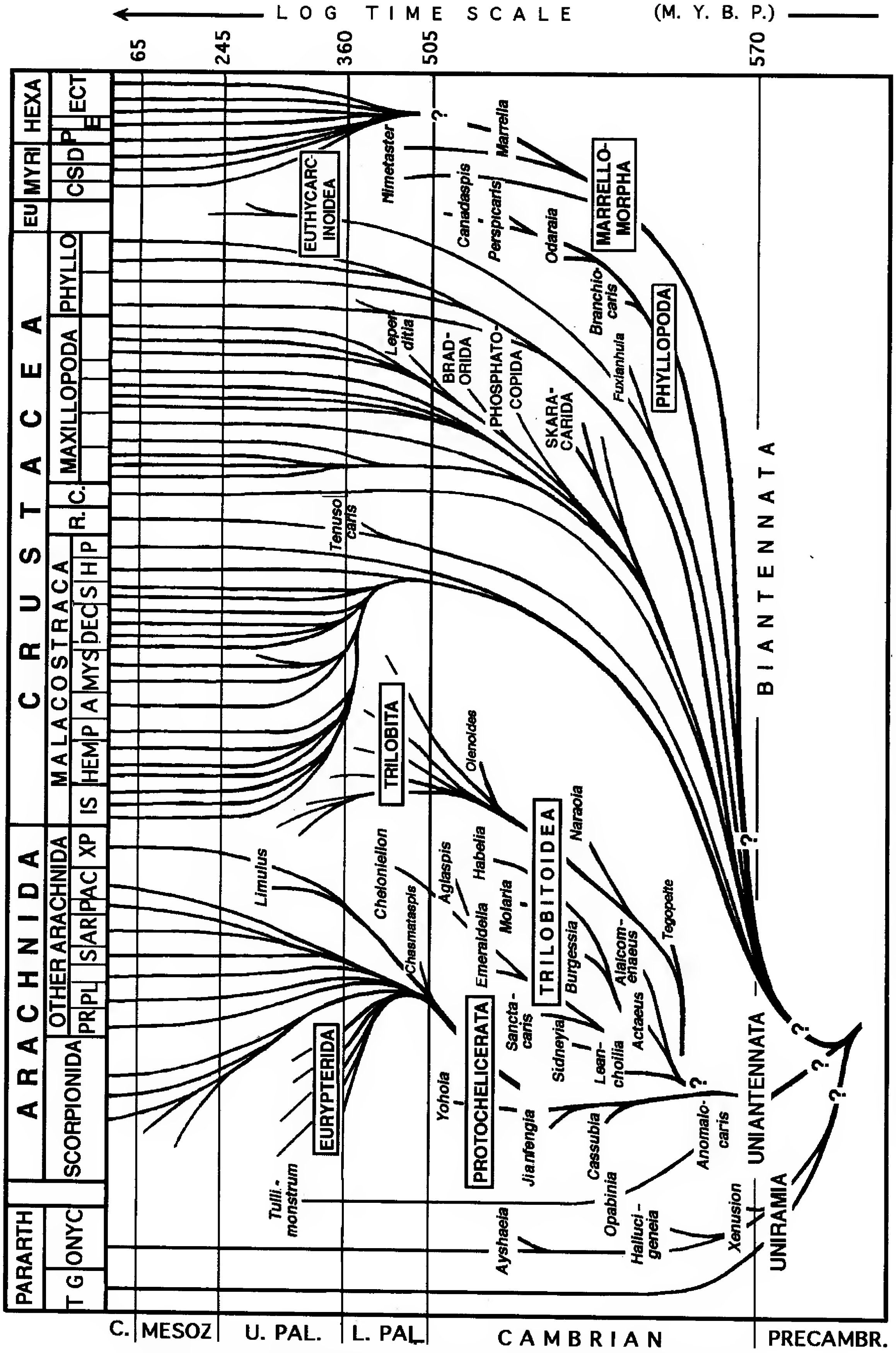


FIG. 10. PHYLOGENETIC TREE OF THE ARTHROPODA EMPHASIZING THE MIDDLE CAMBRIAN FAUNA
(Based partly on Schram (1986) and Bousfield & Conlan (1990))

FIG. 10. PHYLOGENETIC TREE OF THE ARTHROPODA

taxonomic sequence of *Anomalocaris, Yohoia, Chasmataspis,* and the Scorpionida illustrates this evolutionary sequence.

(3) Other types of pre-oral limb development that involved an opposing limb raptorial mechanism on the one hand, and a filamentous sensory structure on the other, did not survive the close of the Paleozoic Era.

(4) The cephalization, or incorporation of masticatory limbs of anterior trunk segments into the head shield, of both uni- and bi-antennate arthropods, proceeded most rapidly during the Cambrian Period. Such a rapid evolutionary process in major taxonomic features may prove to be a direct example of punctuated equilibrium proposed by Eldridge & Gould (1972). However, few aquatic taxa with only 2-4 head somites (e.g., a few Probosciferida, Marrellomorpha) survived beyond the Cambrian, although the euthycarcinoids persisted until the Triassic; some with five somites (e.g., Trilobita) reached the late Paleozoic; whereas groups with 6-7 head somites (e.g. Crustacea, Chelicerata) extended into Mesozoic and Recent times.

(5) Primitively shaftlike and elongate trunk limbs became increasingly distinctly segmented, chitinized, and shortened, especially in benthic forms. A series of forms within the crustacean order Skaracarida (e.g. *Dala, Bredocaris, and Oleandocaris*), the phosphatocopine ostracods, and the naupliar-metanaupliar stages of other maxillopodan crustaceans, illustrate such transformation.

(6) The dorsal shield arises from the first head segment (pre-oral carapace) in primitive, pharyngeal-feeding arthropods. In more advanced, limb-masticatory arthropods (e.g., mandibulates) the carapace (secondarily bivalved) arises from the posterior segment of the head shield that is mandibular in phyllopods and typically maxillary in crustaceans.

(7) With respect to the natatory function of limbs, swimming appendages occur in both post-oral head and trunk regions of very early uniantennates, and larval stages of more advanced arthropods. Coincident with tagmatization of the trunk into thorax and abdomen, and the "cephalization" of feeding limbs in higher taxa, swimming, and respiratory, functions shifted posteriorly from head to thorax and finally to abdomen, as in stomatopods, isopods, and other Malacostraca.

(8) Evolution of the terrestrial myriapods and hexapods from presumed aquatic ancestors apparently involved loss of the second pre-oral head segment and its antennate appendages. In the aquatic environment, those limbs are functionally sensory (see Callahan, 1979), locomotory, or even food gathering. In the terrestrial environment, such limbs presumably became duplicative and mechanically unwieldy, and followed into oblivion the original prothoracic wings of insects. Similarly, in peracaridan crustaceans that have become secondarily terrestrial (e.g., talitrid amphipods, oniscoidean isopods), one of the sensory antennal pairs (first, antennules) has become very much reduced or vestigial, with only one pair (second, antennal) remaining effectively functional. In similar vein, an alternative functional evolution of the head appendages of myriapods and hexapods would countenance the fusion of the first pre-oral limbs to the labrum to form the clypeo-labrum, and the second pair of head appendages, equivalent to the second antennae of crustaceans, have become the monofilamentous antennae of the hexapods. However, embryological and/or paleohistorical (fossil) evidence for such a proposal has not yet been demonstrated.

In summary, in the most successful arthropod groups of modern times, the head shield encompasses anterior limbs of the primordial trunk region, limbs that assist in food capture and mastication. Body tagmatization has become pronounced, and swimming, ambulatory and respiratory functions are relegated increasingly to thoracic and abdominal limbs (see also Schram, 1986). In higher crustaceans (malacostracans), thoracic limbs have become uniramous, cheliform and versatile, and the antennules secondarily bi- or tri-ramous and sensory. In higher arachnids, however (e.g., pedipalpids and phalangids), the prosomal limb gnathobases have become secondarily lost, but feeding mechanisms remain primitive in the retention of chelicerate pre-oral limbs and a suctorial pharynx. In tracheates, the exopods of trunk limbs have been lost. In hexapods, the abdominal limbs have become vestigial or lost entirely, and exites of limbs have secondarily become gills and/or trachaeae in the abdomen, and trachaeae and/or wings in the thorax (see Kukalova-Peck, 1987, 1992). Such fundamental morphological changes in arthropod body form have unquestionably contributed vitally to the ability of modern groups to utilize the diverse organic and plant-related food resources that have evolved mainly in terrestrial habitats, and mainly since the late Paleozoic Era.

Source references for taxonomic and classificatory names and time-scale occurrences in following Tables III-V are: E. L. Smith - unpublished MS "Atlas of Insect Morphology"; L. Størmer (1959) - in Treatise on Invertebrate Paleontology; J Bergström (1979) - "Morphology of Fossil Arthropods"; S. J. Gould (1989) - "Wonderful Life" & source materials; D.E.G. Briggs et al. (1993) - "The Burgess Shale fauna" and source material; L. Delle Cave & A. M. Simonetta (1991)- "Early Palaeozoic Arthropods"; T. Savory (1964) - "Arachnids"; F. R. Schram (1986) - "Crustacea"; and numerous other source papers including arthropod sections in "Synopsis and Classification of Living organisms", McGraw Hill, 1982.

A database for analysis of the paleohistorical occurence of major taxonomic groups is given in Table V (p. 28). Some taxonomic names, especially those relatively recently published or not sufficiently well described (e.g., *Waptia* Walcott, 1912) have been omitted from the lists and the analysis. A complete bibliography of citations of taxonomic names is not included in the references here, but may be found in the Zoological Record or other basic reference texts for the taxa, author names and dates concerned.

TABLE III. SUGGESTED NATURAL CLASSIFICATION OF AQUATIC, ESPECIALLY EARLY PALEOZOIC, ARTHROPODA BASED ON FOOD-GATHERING AND FEEDING MECHANISMS.

PHYLUM ARTHROPODA

I. INFRAPHYLUM UNIANTENNATA, new name (= **MANDIBULOPODA** E. L. Smith "Atlas")
One pair of positionally and embryonically pre-oral head limbs; trunk limbs often gnathobasic.

†SUPERCLASS DICEPHALOSOMATA Sharov, 1966 (L. Camb. - U. Carb)
Pre-oral limbs raptorial, non cheliform, 4-14 segments; post-oral limbs non food-gathering; feeding pharyngeal, assisted by pre-oral limbs; trunk 12+ segmented, pygidial?; limbs locomotory, respiratory; aquatic.
†CLASS ANOMALOCARIDEA Raymond, 1935 (L. - M. Camb.)
Pre-oral limbs paired, 7-14 segmented; 1-3 post-oral head segments; peribuccal teeth present.
†SUBCLASS ANOMALOCARIDATA new (L. - M. Camb)
Pre-oral limbs 11-14-segmented; 3 post-oral head segments; trunk limbs natatory
†Order Anomalocarida Raymond, 1935 (*Anomalocaris* Whiteaves, 1892; *?Hurdia* Walcott, 1912)
†SUBCLASS CASSUBIATA new (L. Camb)
Pre-oral limbs 7-segmented; 1? post-oral head segment; anterior trunk limbs ambulatory?
†Order Cassubiida new (*Cassubia* Lendzion, 1977)

†CLASS PROTOCHELICERATA Strmer, 1944, revised and restricted (L. - M. Camb.)ø
Pre-oral limbs paired, semi-chelicerate, 4-5 segmented; 3 pairs post-oral, biramous ambulatory head limbs.
†SUBCLASS YOHOIIDACEA Henriksen 1928, new status (L. - M. Camb)
Trunk limbs biramous, natatory, respiratory.
†Superorder Yohoiidea Henriksen 1928
†Order Jianfengiida new (*Jianfengia* Hou, 1987) (L. Camb)
†Order Yohoiida Henriksen 1928 (*Yohoia* Walcott, 1912) (M. Camb)

†CLASS PROBOSCIFERIDEA Sharov, 1966 emend (M. Camb - U. Carb)
Pre-oral limbs fused to clawlike (14-segmented) jaws on anterior proboscis; post-oral head segments and peribuccal teeth lacking.
†SUBCLASS OPABINIIDACEA Størmer, 1944 (M. Camb)
†Order Opabiniida Størmer, 1944 (*Opabinia* Walcott, 1912;*?Kerygmachela* Conway Morris et al. 1987)
†SUBCLASS TULLIMONSTRIDEA E. L. Smith "Atlas" (U. Carb)
†Order Tullimonstrida (*Tullimonstrum* Richardson, 1966)

†SUPERCLASS TRILOBITOMORPHA Størmer, 1944, restricted status (L. Camb. - M. Perm.)
Pre-oral limbs filamentous, non raptorial; post-oral head limbs and trunk limbs normally biramous, endopods modified for food-gathering and/or feeding.

†CLASS (SUBCLASS) LEANCHOILIIDACEA Raymond, 1953, new status (L. - U. Camb.)
2-3 pairs post-oral, spinose (or weakly gnathobasic) transitional head limbs; trunk limb endopods transitional; telson large.
†Superorder Leanchoiliidea Raymond, 1935
Head with 2 post-oral segments; pre-oral limbs multi-flagellate; eyes lacking.
†Order Leanchoiliida (*Leanchoilia* Walcott, 1912; *Acanthomeridion* Hou, Chen & Lu, 1989)
†Superorder Alalcomenaeidea Simonetta, 1970
Head with 3 post-oral segments; pre-oral limbs bi-flagellate or with accessory lobe; eyes present.
†Order Actaeida (*Actaeus* Simonetta, 1970)
†Order Alalcomenaeida (*Alalcomenaeus* Simonetta, 1970;

†CLASS (SUBCLASS) SIDNEYIDEA Walcott, 1911, new status (M. Camb.)
Lacking post-oral head segment(s) or limbs; trunk not trilobate, limbs gnathobasic; telson flabellate.
†Order Limulavida Walcott, 1911. (*Sidneyia* Walcott, 1911) (*Saratrocercus* - a larval stage?)

†CLASS TRILOBITOIDEA Størmer, 1955, restricted (L. Camb. - U. Perm.)
3 pairs of post-oral gnathobasic, masticatory head limbs; trunk limbs biramous, endopods gnathobasic.

†**SUBCLASS BURGESSIDEA** Walcott, 1912 (L. - M. Camb)

Trunk lacking lateral pleurae, limbs biramous; tail region with spikelike telson.

- †**Order Burgessiida** Walcott, 1912 (*Burgessia* Walcott, 1912)
- †**Order Molariida** Walcott, 1912 (*Molaria* Walcott, 1912; *Emeraldoides* Simonetta, 1964)
- †**Order Habeliida** Simonetta & delle Cave 1972 (*Habelia* Walcott, 1912; *Thelxiopa; Economocaris)*

TRILOBITOIDEA INCERTAE SEDIS *Tontoia* Walcott, 1912. *Nathorstia* Walcott, 1912;*Retifacies* Hou, Chen & Lu, 1989; *Koumaia* Hou, 1987; *Rhombicalvaria* Hou, 1987; *Helmetia* Walcott, 1917;*Mollisonia* Walcott, 1912;*Urokodia* Hou, Chen & Lu, 1989; *Corcorania* Jell, 1980; *Serracaris* Briggs, 1978?

†**SUBCLASS TRILOBITA** Walch, 1771 (L. Camb - U. Perm)

Trunk segments typically with lateral pleurae (trilobate); tail region pygidial.

- †**Superorder Eotrilobitacea** Whittington, 1977 (L. - M. Camb)
  - †**Order Nectaspida** Raymond, 1920 (*Naraoia* Walcott, 1912) (Incl. *Liwia* & *Tegopelte,* L. Camb)
- †**Superorder Trilobitacea** Walch 1771 (L. Camb - M. Perm)
  - †**Order Agnostida** Kobayashi 1935
  - †**Order Redlichiida** Richter, 1933
  - †**Order Corynexochida** Kobayashi, 1935
  - †**Order Ptychopariida** Swinnerton 1915
  - †**Order Phacopida** Salter, 1964
  - †**Order Lichida** Moore, 1959
  - †**Order Odontopleurida** Whittington, 1959

†**CLASS EMERALDELLIDEA** Raymond, 1935 (M. Camb. - L. Dev.)

5 pairs of post-oral, gnathobasic, masticatory head limbs; trunk limbs biramous, endopods ambulatory.

†**SUBCLASS SANCTICARIDEA** E. L. Smith "Atlas" (M. Camb)

Pre-oral limb biramous; post-oral head limbs raptorial, unlike ambulatory trunk limbs; telson flabellate.

- †**Order Sanctacarida** E. L. Smith "Atlas" (*Sanctacaris* Briggs & Collins, 1988 [=*Utahcaris orion* Conway Morris & Robison, 1988]).

†**SUBCLASS EMERALDELLACEA** Raymond, 1935 (M. Camb - L. Dev)

Pre-oral limb uniramous, filiform; post-oral head and trunk limbs ambulatory and raptorial; telson a spike

- †**Order Emeraldellida** Simonetta & Della Cave, 1975, revised (*Emeraldella* Walcott, 1912)
- †**Order Cheloniellonida** Brioli, 1933 (*Cheloniellon* Broili, 1932) (L. Dev)
- †**Order Aglaspida** (Walcott, 1911) (*Aglaspis* Hall, 1862, revised Briggs et al, 1978) (L. Ord)
  Inclusions: *Aglaspella, Beckwithia, Palaeomerus; Borchgrevinkium; Palaeoniscus, Kodymirus? Strabops?*

SUPERCLASS CHELICERATA Heymons 1901 (L. Ord - R)

Pre-oral limb chelicerate, 3- (occasionally 2- or 4-) segmented; 5 (6) pairs of uniramous post-oral head limbs; trunk limbs uniramous, respiratory.

CLASS MEROSTOMATA Dana, 1852 (L. Ord - R)

Post-oral head limbs gnathobasic, first pair undifferentiated; trunk limbs reduced to book gills; aquatic.

SUBCLASS XIPHOSURA Latreille 1802 (L. Ord -R)

Pre- and post-abdomen strongly differentiated; one pair of compound eyes.

- **Superorder Chasmataspididea** Caster & Brooks, 1956, revised status (L. Ord - Dev)
  Post-abdomen 9-segmented; pre-abdomen 3-segmented?
  - **Order Chasmataspidida** Caster & Brooks, 1950 (L. Ord-Sil) (*Chasmataspis, Pseudoniscus*)
  - **Order Diploaspidida** Caster & Brooks, 1956 revised status (Dev) (*Diploaspis, Heteroaspis*)
- **Superorder Xiphosuridea** Latreille, 1802 (U. Sil. - R)
  Post-abdomen 1-3-segmented; pre-abdomen 7(8)-segmented.
  - †**Order Triopida** Packard, 1886 (L. Ord) (*Triopus*)
  - †**Order Synxiphosurina** Packard, 1886 (incl. *Weinbergina*) (6 pairs post-oral head limbs)
  - **Order Limulina** Richter & Richter, 1929 (Carb - R) (*Limulus* L. 1787; + *Euproops* (Carb))

†SUBCLASS EURYPTERIDA Burmeister, 1843 (L. Ord - Perm)

Pre and post-abdomen not strongly demarcated; 2 pairs compound eyes

†Order Eurypterida Burmeister, 1843 *(Eurypterus)*

†Order Pterygota Clarke & Rudemann, 1912

CLASS ARACHNIDA Lamarck 1801 (Ord. - R)

Post-oral head limbs (secondarily) non-gnathobasic, first often differentiated as pedipalps; feeding chelicerate; anterior trunk limbs forming book lungs or lacking; terrestrial.

SUBCLASS SCORPINIATA Latreille, 1817 (Sil - R)

Order Scorpionida Latreille 1806 (Sil - R)

SUBCLASS PEDIPALPATA Latreille 1906 (M. Dev - R)

Order Palpigradida Thorell, 1881 (Jur - R)

Order Schizomida Petrunkevitch, 1945 (U. Tert - R)

Order Uropygida Thorell, 1882 (U. Carb - R)

Order Amblypygida Thorell 1883 (U. Carb - R)

Order Aranaea Clerck, 1757 (U. Carb - R)

†Order Trigonotarbita Petrunkevitch, 1949 (M. Dev - U. Carb)

SUBCLASS PHALANGIATA Leach, 1915 (U. Carb - R)

Order Solfugida Leach 1815 (U. Carb - R)

Order Acarida Nitzsch 1818 (M. Dev - R)

Order Ricinulida Thorell, 1892 (U. Carb - R)

Order Opilionida Sundevall 1833 (U. Carb - R)

Order Pseudoscorpionida Latreille, 1817 (Olig. - R)

CLASS PYCNOGONIDA Latreille, 1910 (L. Dev - R)

Post-oral head limbs non-gnathobasic, first differentiated as pedipalps; feeding pharyngeal, pre-oral limb assisted; aquatic.

†SUBCLASS PALAEOPYCNOGONIDA E. L. Smith "Atlas" (L. Dev)

†Order Palaeoisopida Hedgepeth, 1978 (*Palaeoisopus* Broili, 1928)

†Order Palaeopantopoda Broili, 1930 (*Palaeopantopus* Broili, 1928)

SUBCLASS PODOSOMATA Leach, 1813 (L. Dev - R)

Order Pantopoda Gerstaeker, 1963 (*Pycnogonum littorale* L.)

TABLE IV. SUGGESTED NATURAL CLASSIFICATION OF BIANTENNATE ARTHROPODS

2. INFRAPHYLUM BIANTENNATA Bergström, 1979 revised (= **MANDIBULATA** Clairville, 1798)

Head with acron and 2 pairs of positionally pre-oral limbs, 2nd pair embryonically post-oral, biramous; 3rd (when present) mandibulate; trunk limbs not gnathobasic.

†SUPERCLASS EUTHYCARCINOMORPHA Handlirsch, 1914, revised status (L. Camb. - Trias)

Head 2(3)-segmented; head shield not maxillary; trunk tagmatized; thoracic limbs primitively biramous, endopods slender, multi-segmented, lacking terminal claws; abdomen limbless, with telson..

†CLASS EUTHYCARCINOIDEA Handlirsch, 1914 (L. Camb - U. Trias)

With the characters of the superclass.

†SUBCLASS FUXIANHUIATA new (L. Camb)

Trunk multi-segmented, segments simple, each with one pair of biramous limbs; telson short.

†Order Fuxianhuiida new (*Fuxianhuia protensa* Hou, 1987)

INCERTA SEDIS: *Chengjiangocaris longiformis* Hou & Bergström, 1991.

†SUBCLASS EUTHYCARCINATA Handlirsch, 1914. (U. Carb - Trias)

Trunk with few (<20) diplo- and/or triplo- segments; trunk limbs uniramous, two per diplo-segment; telson elongate.

†Order Sottixeriformes Schram & Rolfe, 1982 (*Pieckoxerxes piekoae* Starobogatov, 1988)

†Order Euthycarciniformes Schram & Rolfe, 1982 (*Kottixerxes gloriosus* Starobogotov, 1988)

†SUPERCLASS MARRELLOMORPHA Walcott, 1912, new status (M. Camb - L. Dev)
Head 2-4-segmented; head shield spinose or bivalved, not maxillary; mandible, endopod leglike; trunk not tagmatized; trunk limbs undifferentiated, endopods strongly leglike, ambulatory, exopods narrowly lamellate.

†CLASS MARRELLIDEA Walcott, 1912 (M. Camb - L. Dev)
Head 2-3 segmented; head shield with paired spines; telson minute.
†SUBCLASS MARRELLATA Walcott, 1912 (M. Camb)
Head 2-segmented; first post-oral head limbs antenna-like.
†Order Marrellida Walcott, 1912 (*Marrella* Walcott, 1912)
†SUBCLASS MIMETASTERATA E. L. Smith "Atlas" (L. Dev)
Head 3-segmented; first post-oral head limbs leg-like.
†Order Mimetasterida (*Mimetaster* Gurich, 1931)

†CLASS ACERCOSTRACA Lehmann, 1955 (L. Dev)
Head 4-segmented; head shield with carapace.
†SUBCLASS VACHONISIATA E. L. Smith "Atlas" (L. Dev)
Post-oral limbs 3 & 4 leglike, weakly gnathobasic.
†Order Vachonisiida new (*Vachonisia* Lehmann, 1955)

†SUPERCLASS PHYLLOPODA Latreille, 1825 revised, restricted (M. Camb - L Ord)
Head 3-segmented; head shield bivalved, not maxillary; mandible masticatory, not leglike or palpate; trunk 15+ segmented, weakly tagmatized; endopods weakly leglike, exopods broadly lamellate (phyllopodous).

†CLASS BRANCHIOCARIDEA E. L. Smith "Atlas" (M. Camb)
Head 3-segmented; trunk segments numerous (20+), with similar phyllopodous limbs.
†SUBCLASS BRANCHIOCARATA E. L. Smith "Atlas" (M. Camb)
First two pairs of head appendage prominent, 2nd pair cheliform?; carapace normal; tail region bifid.
†Order Branchiocarida E. L. Smith "Atlas" (*Branchiocaris* Briggs, 1976)
†SUBCLASS ODARAIATA Simonetta & Delle Cave, 1975 (M. Camb)
Pre-oral appendages minute, linear?; carapace tubular; tail region trifid.
†Order Odaraiida Simonetta & Delle Cave, 1975 (*Odaraia* Walcott, 1912)

†CLASS (SUBCLASS) CANADASPIDIDEA Novoshilov, 1960 (M. Camb - L. Ord)
Head appearing indistinctly 5-segmented, posterior 2 pairs of limbs similar to trunk limbs; trunk 15-segmented, posterior 7 segments lacking paired appendages.
†Order Canadaspidida (*Canadaspis* Novoshilov, 1960; *Perspicaris* Briggs, 1977;*?Rhebachiella kinnekullensis* Müller 1983 (larval stages)
?Order Hymenostraca Rolfe, 1969 (*Hymenocaris* Salter, 1853) (M. Camb - L. Ord)

SUPERCLASS CRUSTACEA Pennant, 1777 (after Schram, 1986) (M. Camb - R)
Head with pre-oral antenna and 4 post-oral limbs, first antennalike, 2-4 (including mandible) masticatory; head shield maxillary; trunk often tagmatized, limbs often differentiated, specialized; telson present.

CLASS (SUBCLASS) REMIPEDIA Yager, 1981 (M. Dev - R)
†Order Enantiopoda Birshtein, 1960 (*Tesnusocaris* Brooks, 1955) (M. Dev)
Order Nectiopoda Schram, 1986 (*Speleonectes* Yager, 1981) (R)

CLASS BRANCHIOPODA Latreille, 1817 (L. Dev - R)
SUBCLASS SARSOSTRACA Tasch, 1969 (M. Dev - R)
†Order Lipostraca Scourfield, 1926 (M. Dev)
Order Anostraca Sars, 1867 (L. Dev - R)
SUBCLASS CALMANOSTRACA Tasch, 1969 (M. Dev. - R)
Order Notostraca Sars, 1867 (L. Dev - R)

Order Kazacharthraca Novozhilov, 1957 (L. Jur)
Order Conchostraca Sars, 1867 (L. Dev - R)
Order Cladocera Latreille, 1829 (Perm - R)

CLASS (SUBCLASS) CEPHALOCARIDA Sanders, 1955 (R)
Order Brachypoda Birshtein, 1960 (*Hutchinsoniella* Sanders, 1955)

CLASS MAXILLOPODA Dahl, 1956 (L. Camb - R)
†**SUBCLASS SKARACARIDA** Müller, 1983 (M. Camb - U. Camb))
Order Skaracarida Müller, 1983. *Skara annulata* Müller, 1983) (several other, mostly larval genera, e.g., *Dala, Walossekia, Oelandocaris, Bredocaris,*
SUBCLASS OSTRACODA Latreille, 1836 (L. Camb - R)
†**Order Bradoriidae** Matthew, 1902
†**Order Phosphatocopida** K. J. Müller, 1964 (L. Camb. - L. Ord)
†**Order Leperditicopida** Scott, 1961 (U. Camb - U. Dev)
†**Order Palaeocopida** Henningsmoen, 1953 (L. Ord - Trias)
Order Halocyprida Dana 1852 (Sil - R)
Order Platycopida Sars 1866 (L. Ord - R)
Order Cladocopida Sars 1866 (Ord - R)
Order Myodicopida Sars, 1966 (Ord - R)
Order Podocopida Sars, 1866 (Sil - R)
SUBCLASS THECOSTRACA Gruvel, 1905 (M. Camb - R)
Order Facetotecta Gruvel, 1905
Order Rhizocephala F. Müller, 1862
Order Ascothoracida Lacaze-Duthiers, 1880
Order Cirripedia Burmeister, 1834 (M. Camb - R)
SUBCLASS TANTULOCARIDA Boxshall & Lincoln, 1983 (R)
Order Tantulocaridida Boxshall & Lincoln, 1983
SUBCLASS COPEPODA Milne-Edwards, 1840 (Cret - R)
Order Calanoida Sars, 1903
Order Harpacticoida Sars, 1903
Order Cyclopoida Burmeister, 1834
Order Misophrioida Gurney, 1933
Order Monstrilloida Sars, 1903
Order Siphonostomatoida Thorell, 1859 emend Sars 1918
Order Poecilostomatoida Thorell 1859
SUBCLASS LINGULATULIDA Frolich, 1789 (=Pentastomatida Rudolphi 1819) (R)
Order Cephalobaeniuda Heymons & Vitzthum, 1936
Order Porocephalida Heymons & Vitzthem, 1936

†**CLASS (SUBCLASS) THYLACOCEPHALA** Pinna, Arduini et al, 1982. (Camb? L. Sil - Cen)
†**Order Concavicarida** Briggs & Rolfe, 1983 (L. Sil - Cen)
†**Order Conchyliocarida** Secretan, 1983 (Camb? - Jur)

CLASS MALACOSTRACA Latreille 1806 (Dev - R)
SUBCLASS PHYLLOCARIDA Packard, 1879 emended (Dev - R)
†**Order Archaeostraca** Claus, 1888
†**Order Hoplostraca** Schram, 1973
Order Leptostraca Claus, 1880 (see also Dahl, 1984)
SUBCLASS HOPLOCARIDA Calman 1904 (U. Dev - R)
†**Order Aeschronectida** Schram, 1969 (Carb)
†**Order Palaeostomatopoda** Brooks, 1955 (U. Dev - L. Carb)
Order Stomatopoda Latreille, 1817 (Carb - R)
SUBCLASS EUMALACOSTRACA Grobben, 1892 (modified from Schram, 1986) (U. Dev - R)
Superorder Syncarida Packard, 1885 (U. Carb - R)
†**Order Palaeocaridacea** Brooks, 1962

Order Anaspidacea Calman, 1904
Order Bathynellacea Chappuis, 1915
Order Stygocaridacea Noodt ,1964
†**Superorder Belotelsonidea** Schram, 1981
†**Superorder Waterstonellidea** Schram, 1981
†**Superorder Eocaridacea** Brooks, 1962
Superorder Thermosbaenacea Monod, 1927
Superorder Mysidacea Boas, 1883
Order Lophogastrida Boas, 1883
†**Order Pygocephalomorpha** Beurlen, 1930
Order Mysida Boas 1883
Superorder Amphipoda Latreille, 1916
Superorder Hemicaridea Schram, 1981 emended
Order Spelaeogriphacea Gordon, 1957
Order Mictacea Bowman et al. 1985
Order Cumacea Kroyer, 1846
Order Tanaidacea Dana, 1853
Superorder Isopoda Latreille, 1817
Superorder Eucarida Calman, 1904
Order Euphausiacea Dana, 1862
Order Amphionidacea Williamson, 1973
Order Decapoda Latreille, 1803

SUPERCLASS MYRIAPODA Latreille, 1796 (Sil - R) (Essentially terrestrial; not detailed here)

Head with embryonic acron, pre-oral antenna, 5 post-oral pairs of masticatory limbs (1st post-oral embryonic); trunk not tagmatized, with more than 20 pairs of ambulatory limbs, ending in telson.

CLASS SYMPHYLA Ruder, 1880 **(1 subclass)** (Olig - R)
CLASS CHILOPODA Latreille, 1802 **(2 subclasses)** (M. Dev - R)
CLASS PAUROPODA Lubbock, 1866 **(1 subclass)** (R)
CLASS DIPLOPODA Gervais, 1844 **(3 subclasses)** (Sil - R)
†**CLASS ARTHROPLEURIDEA** Zittel, 1848 **(1 subclass)**(L. Dev - U. Carb)

SUPERCLASS HEXAPODA (L. Dev. - R.) (Essentially terrestrial; not detailed here)

Head with acron + pre-oral antenna, 4 post-oral pairs masticatory limbs (1st post-oral embryonic, 2nd mandibulate; trunk tagmatized; thorax with 3, abdomen with 11 (max.) pairs ambulatory limbs; telson embryonic.

CLASS PARINSECTA (2 Subclasses: Collembola, Protura) (L. Dev - R)
CLASS INSECTA (2 Subclasses Entognatha, Ectognatha) (U. Carb - R).

TABLE V. NUMBERS OF HIGHER ARTHROPOD TAXA SINCE CAMBRIAN TIMES.

ARTHROPOD INFRAPHYLA	PERIOD									IV TOTALS		
	I CAMBRIAN (545-495 mybp)			II LATE PALEOZOIC (~300 mybp)			III TERTIARY-RECENT (0-30 mybp)					
	SPCL.	CL.	SBCL.	SPCL.	CL.	SBCL.	SPCL.	CL.	SBCL	SPCL.	CL.	SBCL.
UNIANTENNATA	2	8	11	3	5	8	1	3	5	3	10	18
BIANTENNATA	4	6	9	5	11	24	3	12	24	6	18	34
TOTAL ARTHROPODA	6	14	20	8	16	32	4	15	29	**9**	**28**	**52**

Arthropod Diversity and Evolutionary Trends

Table V summarizes (from Tables III & IV) the number of higher arthropod taxonomic categories, recognized here at superclass (SPCL), class (CL) and subclass (SBCL) levels, that are represented by known genera and species of the Cambrian, late Paleozoic and Tertiary-Recent Periods. Analysis of the changing numbers with geological time reveals interesting and perhaps significant evolutionary trends.

Despite the very great difference in numbers of species known for each of the three time-scale samplings (Cambrian $\sim 10^2$ species; Late Paleozoic- $\sim 10^4$+species; Tertiary-Recent - $\sim 10^6$ + species), the numbers of higher taxa are of comparable orders of magnitude for all categories. In the 600-million-year time span since the presumed dawn of arthropod life (Ediacrian, Vendian), we here categorize only 9 superclasses, 28 classes and 52 subclasses to encompass the entire known fauna, past and present, of well over one million described species (Table V, Col. IV, bottom row). Fully one-third of the early subclasses is known from only 1-10 species, a fact suggesting the likelihood of further new discoveries, at that level or higher, among incompletely described or totally new fossil material. Only one of the 9 superclasses (Crustacea), one of the 28 classes (Maxillopoda) and only two of the 52 subclasses (Ostracoda, Thecostraca) have actually been recorded throughout this immense paleontological range. To this meager total we might add the Chelicerata but it is presently confirmed not earlier than Lower Ordovician. However, further analysis of Paleozoic fossil material is expected to extend the time range of extinct species forwards, and recent species (especially minute, soft-bodied forms), backwards in time. Thus, the morphologically primitive Remipedia and Cephalocarida may have originated during Cambrian times, despite their very limited or non-existent fossil records (see Hessler, 1984). Aquatic larval stages of some other classes of Crustacea and of the merostomatid uniantennates (e.g., phyllocarid and trilobite larvae, respectively), tend to recapitulate adult morphology of extinct, but related, Cambrian categories.

Thus, by the Cambrian Period, 67 % (6/9) of the superclasses, but only ~50% (14/28) of the classes and ~38% (20/52) of the subclasses had evolved. By the late Paleozoic, perhaps the heyday of arthropod evolution generally, nearly all (8/9) the superclasses, and ~60% (16/28; and 32/52) of all classes and subclasses were represented. Today, however, scarcely half (4/9 and 15/28) the superclasses and classes persist, and the percentage of subclasses, 56% (29/52), has also dropped slightly.

If trends are analysed according to infraphylum for each time interval, for the uniantennates the percentages were highest during the Cambrian, with 33% (2/6) of the superclasses, 57% (8/14) of the classes, and 55% (11/20) of the subclasses. However, the group decreased markedly in importance by the late Paleozoic (only 37% of superclasses, ~31% of classes, and ~25% of subclasses), and is lowest today (25% of superclasses, ~20% of classes, and only ~17% of subclasses). By contrast, the biantennates increased steadily from lowest values in the Cambrian (67% of superclasses, 43% of classes and 45% of subclasses), through the late Paleozoic (63% of superclasses, ~70% of classes, and ~67% of subclasses), to maximum dominance today (75% of superclasses, ~80% of classes, and ~83% of subclasses).

These changes in relative numbers of the two arthropod infraphyla may reflect the impact of the evolution of vascular plants during Silurian-Devonian and later periods (Kukalova-Peck, 1987). That event provided an enormous new food resource in both aquatic and terrestrial environments. These nutrients could be exploited by the omnivorous aquatic crustaceans and terrestrial myriapods and hexapods by direct adaptation and diversification of feeding morphology and style (as in malacostracan crustaceans, and winged insects). By contrast, the uniantennates were more or less "locked into" their mainly carnivorous, and some detritivorous life styles; they could take only indirect advantage of this food resource, and only by developing new predatory morphologies and life styles, especially within the terrestrial environment. They are now a secondary part of the terrestrial, and a minute relict part of the aquatic, arthropod fauna.

With respect to the level of arthropod disparity during Cambrian times, the positions of both Gould (1989) and proponents to the contrary (e.g., Ridley, 1993; Wills et al. 1994) receive support from the present analysis. Thus, of 9 "all-time" arthropod superclasses, 7 (including Chelicerata) were represented in Cambrian and Lower Ordovician faunas, but only 4 are represented in the Recent fauna. Especially remarkable is the fact that Cambrian arthropods were entirely aquatic, and were represented by less than 100 species from a very limited series of marine habitats. The two superclasses missing from the Cambrian record, the Myriapoda and the Hexapoda, are both essentially terrestrial. Thus, if only aquatic faunas are considered, the disparity level of Cambrian arthropods is more than 3 times greater (7 vs. 2 superclasses) than today.

On the other hand, at class level, disparity levels are similar (14 vs. 15), and at subclass level, the Recent arthropod fauna is about 50% richer (29 vs. 20). Furthermore, all of the arthropod, or arthropodlike, species of the Burgess Shale, designated by Gould (1989) and Briggs et al. (1993) as new (or probably new) at phylum and/or infraphylum levels, can be adequately encompassed within existing class and/or superclass categories.

Thus, it is concluded here that, during the entire evolutionary history of the Arthropoda, disparity levels were at or near maximum during the Cambrian Period. Such a high level, close to the starting point of the arthropod fossil record, is consistent with the probable correctness of the evolutionary theory of punctuated equilibrium (Eldridge & Gould, 1972). Since invertebrate faunas of early "explosive evolutionary" times were not described comprehensively until the early 20th century (e.g., Walcott (1912), and later), Charles Darwin (1859) may be excused for missing that part of the evolutionary story.

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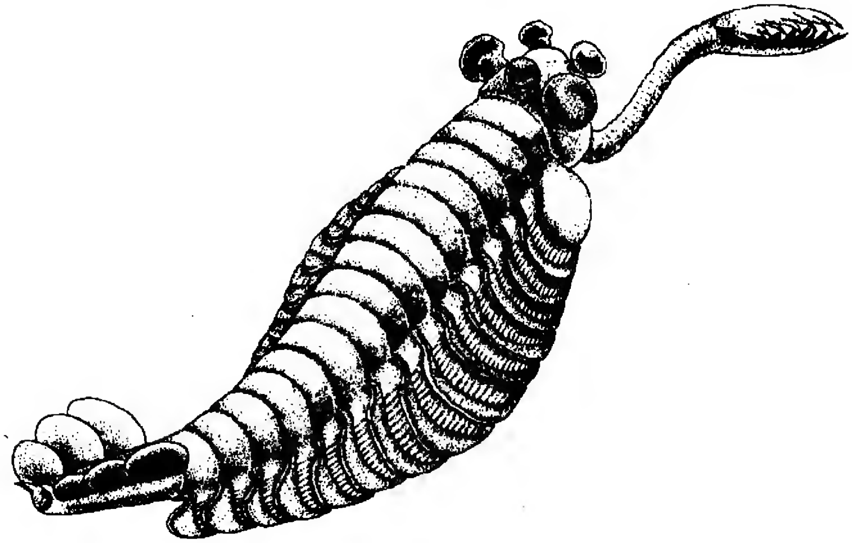

***Opabinia regalis* Walcott**

Middle Cambrian Arthropod

(Marianne Collins illustration, modified from Gould, 1989)